VOL. XLIII, NO. 505 JANUARY, 1909

THE AMERICAN NATURALIST

A MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

CONTENTS

		Page
I.	Juvenile Kelps and the Recapitulation Theory. Professor ROBERT F. GRIGGS.	5
II.	The Larva and Spat of the Canadian Oyster. . . . Dr. J. STAFFORD.	31
III.	Shorter Articles and Correspondence : Some Notes on the Traditions of the Natives of Northeastern Siberia about the Mammoth : WALDEMAR JOCHELSON. Age of Trotting Horse Sires. F. R. MARSHALL. The Occurrence of *Batrachoceps attenuatus* and *Autodax lugubris* in Southern California. WILLIAM A. HILTON	48
VI.	Notes and Literature : *Experimental Evolution*—The Effect of the Environment upon Animals, Dr. FRANK E. LUTZ. *Experimental Zoology*—The Influence of the Size of the Egg and Temperature on the Growth of the Frog, SERGIUS MORGULIS. *Parasitology*—Cestodes of Birds, Professor HENRY B. WARD	55

THE SCIENCE PRESS

LANCASTER, PA. GARRISON, N. Y.

NEW YORK : SUB-STATION 84

The American Naturalist

MSS intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS

Lancaster, Pa. Garrison, N. Y.

NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

Important New Scientific Books

PUBLISHED BY THE MACMILLAN COMPNY

Botany

The Origin of a Land Flora. A Theory based upon the facts of Alternation. By F. O. Bower, Sc.D., F.R.S. With numerous illustrations.

Cloth, gilt top, xi+727 pp., illus., index, 8vo, $5.50 net.

Note.—A profound study in the morphology of the lowest forms of plants, with special reference to the development of their reproductive systems. The author endeavors to show that the present land flora has originated from an aquatic ancestor, and traces the methods of specialization to the land habit, and the establishment of the forms of the higher plants. A book of the highest importance not only to botanists but to biologists in general.

NEW AND STANDARD HAND-BOOKS ON AGRICULTURE, ETC.

Elements of Agriculture, Southern and Western. By W. C. Welborn, B.S., M.S., M.P.A.

Cloth, xvi+329 pp., illus., appendix, glossary, index, 12mo, $.75 net.

Note.—This is a thoroughly modern treatise on farming as practiced in the Gulf States, from the point of view of the scientific agriculturist. It is adapted to school use, but is of practical service to any farmer in that part of the country. The author is vice-director of the Texas Experiment Station.

Re-issues of the highly valued Hand-Books known as the Garden Craft and Rural Science Series, edited by L. H. BAILEY, of Cornell University, Editor of "Cyclopedia of American Horticulture," "Cyclopedia of American Agriculture," etc.

The Principles of Fruit Growing. By L. H. Bailey.
Tenth Edition, $1.50 net, by mail $1.66.

Irrigation and Drainage. By F. H. King.
Fifth Edition, $1.50 net, by mail $1.68.

Principles of Vegetable Gardening. By L. H. Bailey.
Sixth Editron, $1.50 net, by mail $1.68.

Bush Fruits. By Fred W. Card.
Fourth Edition, $1.50 net, by mail $1.66.

Fertilizers. By Edward B. Voorhees.
Tenth Edition, $1.25 net, by mail $1.38

Farm Poultry. By Geo. C. Watson.
Sixth Edition, $1.25 net, by mail $1.42

Published By **The Macmillan Company** 64-66 5th Ave., New York

THE AMERICAN NATURALIST

QK1
.A427
v.43
1909

THE AMERICAN NATURALIST

A Monthly Journal

Devoted to the Advancement of the Biological Sciences

With Special Reference to the Factors of Evolution

VOLUME XLIII

ARDEN
1910

NEW YORK
THE SCIENCE PRESS
1909

PRESS OF
THE NEW ERA PRINTING COMPANY
LANCASTER, PA.

THE
AMERICAN NATURALIST

VOL. XLIII *January, 1909* No. 505

JUVENILE KELPS AND THE RECAPITULATION THEORY. I.

PROFESSOR ROBERT F. GRIGGS
OHIO STATE UNIVERSITY

I. THE DEVELOPMENT OF CERTAIN KELPS

A. *Renfrewia*[1]

FOR the preparation of a former article (Griggs, '06) on Renfrewia the writer had no very young plants, but during the summer of 1907 he was enabled to collect a full series at the Minnesota Seaside Station, Port Renfrew, B. C. This material is of interest for the study of the development of this, the most primitive of the kelps in comparison with the more complex forms.

The smallest specimen found, which measures a trifle less than 4 mm. (Fig. 1), is not certainly determinable. But one 13 mm. long (Fig. 2) had already developed a peculiar swelling of the basal region which characterizes the young plants. The primitive disc of most kelps and of Renfrewia up to this age is rather flat and sharply separable from the stipe, which ascends cleanly without tapering from the top of the disc. In Renfrewia, however, the basal region of the stipe (the region which in other kelps develops hapteric outgrowths) increases in size. As the plant grows this swollen region becomes more prominent till in plants 8 cm. long (Fig. 11) the

[1] Since publishing the original account of *Renfrewia parvula* in 1906 I have found that it is apparently conspecific with Setchell's ('01) *Laminaria ephemera* earlier described from the California coast. Accordingly Setchell's name replaces mine and the plant becomes *Renfrewia ephemera* (Setchell). Cf. Setchell, '08 b.

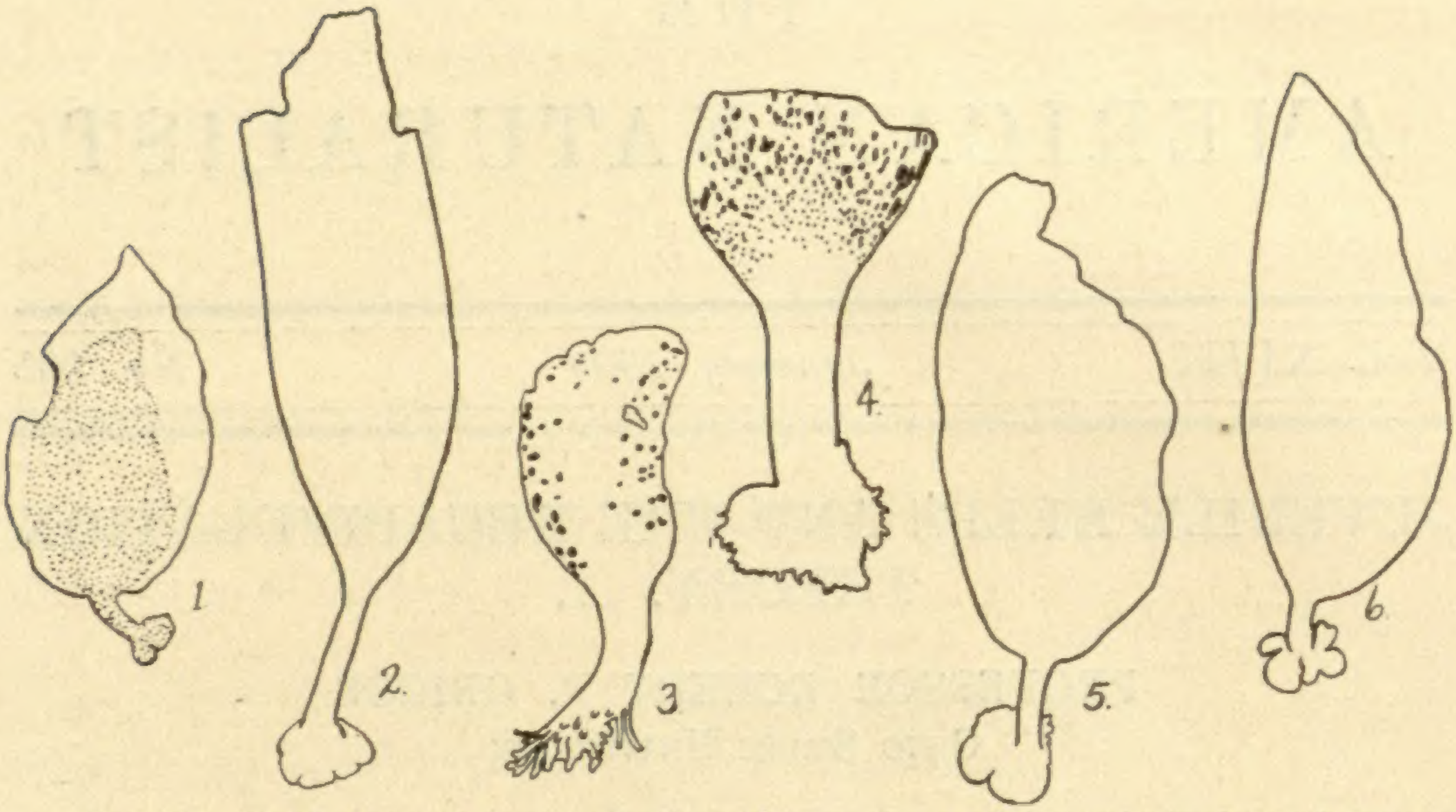


FIG. 1. Renfrewia, 4 mm., shading shows the position of single and many-layered areas in the lamina, holdfast without basal cone.

FIG. 2. Renfrewia, 13 mm., lamina many-layered throughout basal cone beginning to appear.

FIG. 3. Lessoniopsis, 1.1 mm., lamina about four-layered, spots already shown in the cortex, holdfast not developed, plant apparently anchored by filaments.

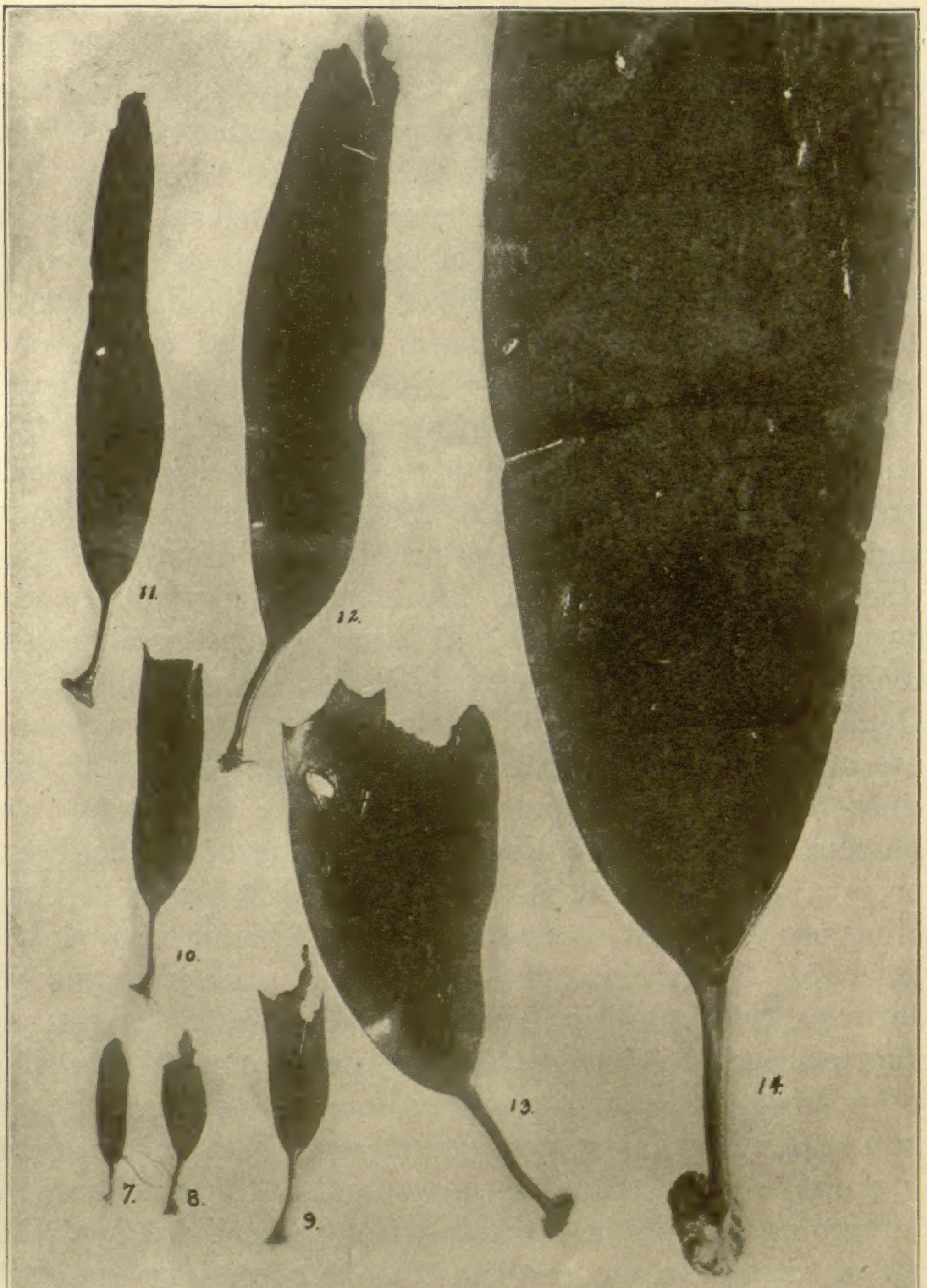
FIG. 4. Lessoniopsis, 2.3 mm., spots in the lamina larger and more evident distally, but still small near the transition region, indicating that growth is already localized, primitive disc developing at base of stipe.

FIG. 5. Hedophyllum, 2.3 mm., showing the much-lobed primitive disc.

FIG. 6. Hedophyllum, 10 mm., lobes of primitive disc grown into the primitive hapteres.

holdfast is an almost straight-sided cone 5 mm. in diameter and of about equal height. Though apparently insignificant this character makes it easy to pick out Renfrewia from other kelps while yet very small. So far as the writer is aware it is not present in any other kelp.

After the plant has reached about a decimeter in length the basal cone ceases to increase and later is lost in the growth of the stipe (Fig. 12). At the same time the disc begins to enlarge and spread out on the substratum, giving a firmer hold for the increasing lamina above. This enlargement is clearly in the region of the primitive disc and not in the conical basal swelling above, which remains part of the stipe. These two tendencies of growth working together usually cause the sharp distinction between the holdfast and stipe to reappear, and in plants more than 15 cm. long the conical base is seldom prominent (Fig. 13). In adults the disc becomes very flat and thin by its continued extension (Fig. 14).



FIGS. 7–11. Renfrewia, series of young plants showing the development of the basal cone. Four fifths natural size.

FIGS. 12–13. Renfrewia, older plants showing the gradual disappearance of the basal cone with increase in size. Four fifths natural size.

FIG. 14. Renfrewia, base of an adult plant, fruiting area extending over almost the entire lamina, its margin indicated by shadows here and there, holdfast showing primitive hapteres. Four fifths natural size.

Some speculations as to the nature and significance of this cone may be of interest. Of all the kelps Renfrewia and Cymathere are the only ones in which the mature holdfasts are restricted to the primitive disc region. In the development of the latter genus, as traced by the writer ('07), there is no indication of such an organ as can be seen by an inspection of the figures then published. Phyllaria and Saccorhiza differ in their holdfast characters from all the other genera. Instead of putting out hapteres directly from their stipes they develop bulbous "rhizogens" which form ring-like collars around the stipe. From these the hapteres are formed by unequal growth along their margins. Though the rhizogen in both genera is separated from the primitive holdfast by a distinct interval on the stipe, it is essentially similar to the basal cone of Renfrewia which we may consider as an incipient rhizogen. This would indicate some leaning of Renfrewia toward the Phylariatæ; but its paraphyses are of the typical clavate form not at all similar to the linear ones of that group. Whether this basal cone is a nascent organ representing the beginning of the holdfast or is a vestige of a Saccorhiza-like rhizogen is a puzzling problem. At some stage in their history the rhizogens of Saccorhiza and Phyllaria probably passed through this condition and remained for a longer or shorter period without further development. On the other hand, the obscuring of the cone in Renfrewia when adult might suggest a vestigial organ. Perhaps the best hypothesis is that Renfrewia was cut out from the main advancing phylum of the kelps, isolated and fixed, at the stage where the tendency to form a secondary holdfast was just beginning to manifest itself.

The tissues of the many-layered lamina of Renfrewia are apparently acquired after the fashion of other kelps, but in Renfrewia the many-layered lamina begins its development in smaller plants than in the Phylariatæ including Cymathere. Even in the smallest specimen (Fig. 1) there is only a small portion of the one-layered blade remaining around the edge of the lamina. In the

13 mm. specimen (Fig. 2), the whole lamina is many layered without any signs of the one-layered portion persisting around its edges. Apparently the embryonic lamina is almost wholly transformed into the adult blade. Like the adult, these young plants are light colored and delicate in texture. They are narrowly elliptical in shape, cuneate at the base and rounding to the apex when not badly abraded.

Except for the basal cone of the stipe young plants 15 mm. long in all characters are like the adult. The adult is larger but the proportions remain the same. Even in the histology there is probably very little difference, for, as described below, Renfrewia develops very imperfectly the complex tissue system which characterizes the higher kelps. What differentiation of tissues appears is probably present long before adult size is reached. Were it not for their reproductive maturity it would be difficult to demonstrate that the adults were mature and not merely larger juvenile forms (Figs. 16, 17); and they have been mistaken by competent observers for juvenile forms of some other kelp.

B. *Lessoniopsis*

Lessoniopsis is a monotypic genus ranging along the Pacific coast from California to Vancouver Island. It was founded by Reinke ('03) to receive *Lessonia littoralis* Farlow and Setchell (see Setchell, '03) which differs from Lessonia in the marked dimorphism of the laminæ, as described below.

The juvenile forms of Lessoniopsis are extremely abundant during July and August at the Minnesota Seaside Station. They grow in clumps of many individuals of all ages. As often as not these clumps start upon the stipes of other kelps, so that one can obtain many hundred specimens simply by cutting off a few old Laminaria stipes. Though the mature plants are often single, it is not at all unusual to find several large plants fused together, as was noticed by Reinke. The reason for this habit of growth of the sporelings is a matter of some in-

terest. There is no difference, as far as the writer is aware, between the fruiting habits of this and other kelps. In quiet water the fragments of any fruiting lamina torn off by the waves might lie undisturbed on the bottom and the spores might germinate close to the point of liberation. But this kelp is a cumaphyte growing exclusively in the strong surf, and it is in surf-scoured situations that the young plants are found best developed. This would lead one to look for some method of basal branching or possibly budding of new laminæ from the holdfast, as is known in a few kelps which have "rhizomes." But though hapteres and stipes are occasionally so completely grown together as to appear branches of one plant, no evidence of such branching in the young plant has been observed and the writer must conclude that the clusters are due to starting of many spores at one point.

The young plants forming these clumps are thickly splashed with checks of dark brown on the lighter color of the body of the lamina. This is most conspicuous in plants about 10 cm. long and is clearly brought out in the photographs (Figs. 15, 21). As they grow older the spotting tends to disappear, but traces of it can usually be found in specimens of any age. No other kelp of the region is similarly marked except Pterygophora, in which the spots when present are much less distinct. As this appearance arises very early it is of the utmost service in identifying the plants while yet too young to have developed any characters of the adult.

The smallest specimen found (Fig. 3) measured about 1.1 mm. in length. It was attached to the hapteres of another plant of the same species twenty or thirty times as long. When loosened from its hold it came away with a mass of filamentous material which completely enveloped its base. In this tangle there was a considerable portion of foreign matter; but the appearance of the finer strands was that of a protonema-like felt organically connected with the young kelp which seemed to spring from it like the gametophore of a moss. On teasing this away it was seen that the primitive disc had not yet developed.

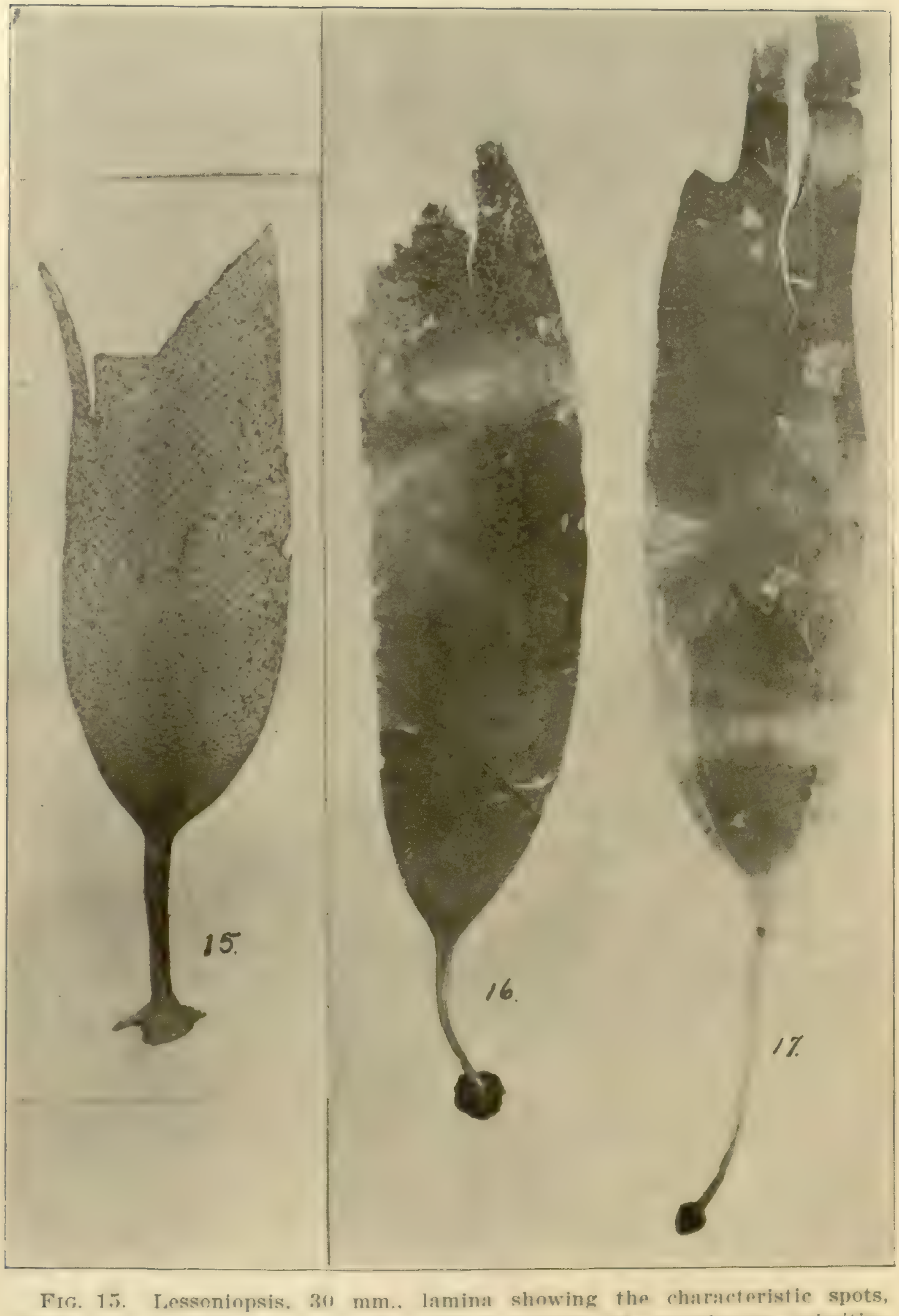


FIG. 15. Lessoniopsis, 30 mm., lamina showing the characteristic spots, midrib just beginning to appear, holdfast formed by conspicuous primitive hapteres.

FIGS. 16–17. Renfrewia, adult, showing similarity to Lessoniopsis when young, fruiting area covers almost the entire lamina in Fig. 16, but in Fig. 17 occupies only a small area at the base and hence clearly discernible, spots in Fig. 16, due to epiphytic algæ. About one half natural size.

The base of the stipe was but slightly larger than the portion above and gave off a large number of filamentous processes, some of which seem to have pressed against the substratum, while others apparently connected with the filaments around the base. Notwithstanding its small size this specimen had a well-developed stipe about a dozen layers of cells in thickness. The internal cells are considerably elongated, though not, as far as can be seen by focusing, differentiated into a pithweb. The lamina was already several cells in thickness even at the edge. Since it was but little frayed, it hardly seems possible that there could have been any remnant of the one-layered lamina which had not been transformed into the many-layered adult blade. In this respect Lessoniopsis would stand at the opposite extreme from Cymathere, in which a large portion of the embryonic lamina is not changed, but continues to grow and persists until the plant is more than 20 cm. long.

The next larger specimen (Fig. 4) measures 2.3 mm., but its true length must have been about 5 mm., for it is sharply truncated a little above the base of the lamina. The holdfast of this specimen was enlarged to form a fairly well developed primitive disc, the base of which was, as in the first specimen, more or less imbedded in a mass of filaments apparently belonging to the kelp. The lamina was much thicker and the spots were seen to be in two layers, one on each side, just beneath the epidermis. In the smaller specimen (Fig. 3), where one spot overlapped another, the two layers could also be made out, but the difference in focus was so slight as to make it appear that they lay in contact, indicating that the lamina was four cells in thickness. In the larger specimen they were separated by a considerable interval which indicated a decided development of the pithweb and cortex. Toward the extremity of the lamina the pigmented spots were very dark and most of them were considerably elongated. They still consisted, however, for the most part, of single cells. Farther back in the transitional region, they were lighter in color, round and more

like those of the first specimen (see Fig. 3). This shows that the region of growth had been definitely localized as a meristem at the base of the lamina (as in the mature plant), while further out in the lamina growth was taking place mainly by the enlargement of cells already formed.

From this point on the development of the species was illustrated by many specimens of all ages. The first marked change was the enlargement of the primitive disc. In a specimen 30 mm. long (Fig. 15) the disc had reached a diameter of 4 mm. At this stage it bears a striking resemblance to that of the adult Renfrewia, being very flat and closely appressed to the substratum. As in that genus, the growth which causes the enlargement becomes localized in certain regions, giving the disc a crenate margin. In places the localization had become sufficiently pronounced to give rise to definite primary hapteres exactly as described by MacMillan ('99) for young plants of Nereocystis and by the writer in the adults of Renfrewia and Cymathere. These primary hapteres are of course all restricted to the primitive disc. Soon after this stage the secondary hapteres begin to arise around the base of the stipe and become very abundant, quickly obliterating the primitive holdfast. The age at which branching and differentiation of the midrib appear varies greatly. Sometimes the plant may reach a length of 80 mm., with only the beginnings of the midrib and of the splitting to form the first branch (Fig. 21); while in one plant of 160 mm. the perforation of the midrib for the branch had only just been accomplished (Fig. 22). On the other hand a specimen (Fig. 19) measuring only 18 mm. showed the position of the perforation plainly marked out. The first appearance of the midrib is indicated by two straight lines extending from the transition region up into the lamina (Fig. 20). The lamina between them grows thicker and takes on the characters of the midrib, which gradually extends toward the tip. But usually for a long time the two edges are more pronounced than any other portion of the rib.

As is well known, the whole subfamily, the Lessoniatæ,

FIGS. 18–23. Lessoniopsis. Four fifths natural size.

FIG. 18. Young plant at about the same stage as Fig. 15 to which is attached another intermediate between it and that shown in Fig. 4.

FIG. 19. Plant grown in heavy surf, holdfast very large; plant dwarfed, indentation for first branch already appearing in the transition region.

FIG. 20. Plant from quiet water grown to an unusually large size, with no indication of branching, midrib just forming.

FIG. 21. Similar to the last except for the beginning of the perforation.

FIG. 22. Perforation complete.

FIG. 23. Primary branching complete, perforations formed for second branches, inner side of new laminæ beginning to form from the divided midrib.

to which Lessoniopsis belongs, is characterized by the repeated splitting of the original unbranched lamina till the plant comes to have a cluster of many leaves. The method of this branching is peculiar to the kelps. Instead of forking at the tip or sending out a new shoot as a lateral proliferation, the branching begins in the transition region between the stipe and the lamina and extends upward until it reaches the tip of the lamina, thus splitting it, while the stipe is divided, to a greater or less extent in the different genera, by the downward extension of the same process. This method of branching is the necessary consequence of the position of the meristem, which is situated at the junction of lamina and stipe, so that all new growth is intercalated between the older portions of both. It is obvious, therefore, that any new structure, such as a branch, must originate in this region of growth.

In Lessoniopsis the first indication of branching appears in a slight depression in the midrib on each side of the lamina at the transition region. These depressions or pits enlarge and deepen until they meet and form a perforation almost exactly at the base of the lamina. It will be readily seen that if the split extended uniformly upward through the midrib, it would result in two unsymmetrical falcate laminæ each with a rib along its inner side. This, however, is not usually the case, for new tissue forms between the divisions of the midrib and soon duplicates on the inner side the outer edge of the lamina (Fig. 24, *a*). Thus each of the new laminæ is approximately symmetrical with respect to its midrib. In the stipe the branching is carried far enough to involve the whole of the meristem, so that future lengthening is almost completely confined to the stipes of the branches.

Before the new laminæ have completely separated there usually begins to appear at the base of each, the second split, which is carried to its completion in the same manner as the first. Thus branching continues again and again so long as the plant lives. Since all the splitting is dichotomous, the result should be a flat fan-shaped plant,

FIGS. 24–26. Older Lessoniopsis. About one sixth natural size.

FIG. 24. Plant several times branched; at *a* the process of the formation of the inner side of the divided lamina from the midrib is clearly indicated.

FIG. 25. Plant with about 25 laminæ, original dichotomy plainly shown.

FIG. 26. Plant still undersized but with the characters of the adult; one branch is lifted out by a background to show the sporophylls (*s*) and their relation to the ordinary laminæ, which show the beginnings of division at their bases as in the younger forms.

and sometimes this form is attained even in very old plants, especially those growing in the quieter places, but usually the stipes twist more or less and spread out in all directions, giving the plant a tree-like aspect.

There is no change in this habit of growth until the plant has attained a considerable age. But long before it reaches its full size there appears another kind of lamina among the narrow ones with midribs. These lack the midribs and are much wider, with conspicuously rounded or subcordate bases. The ribbed laminæ are always sterile, but these wider ones become sporophylls. Consequently after their sporangia are discharged they slough off and disappear, leaving for a time scars on the stipe. The origin of these sporophylls is evidently different from that of the ordinary laminæ. Since very few new sporophylls are developed during the summer, at

least at Port Renfrew, it seems probable that their production is a seasonal phenomenon taking place only for a limited period before the fruiting season. However they are formed, they do not reach their full size at first. The youngest are always shorter and narrower than the older and entirely lack the characteristic base. Some of the smallest remind one of the young sporophylls of Pterygophora and have the appearance of being outgrowths from the meristem as in that species, but the writer does not feel sure that they are normal. Further information on the origin of the sporophylls will be very welcome because of its importance in determining the relationships of this plant to the other genera of kelps.

At length, by branching and production of sporophylls a plant is formed with several hundred laminæ, in extreme cases reaching lengths of a meter, while the whole plant is often two meters long. The stipe at the base becomes 10–20 cm. in thickness and is marked with many annual rings of growth. The holdfast clings so tenaciously to the rocks that it will support a man's weight. On a flat bottom the plants stand upright, but they hang down when growing on an overhanging cliff, as in the photograph (Fig. 27). As in all water plants, their only way of maintaining themselves in the strong currents in which they live is by bending before them. Accordingly, rigidity is developed only in very large basal portions of the stipe, while the terminal branches have not sufficient stiffness to support the plant when out of the water. Lessoniopsis thrives only in places where the surf is very heavy and is there found along with Postelsia, the sea palm, the most typical of all the cumaphytes, but it does not withstand drying so well as that plant and consequently grows at a considerably lower level.

C. *Egregia*

To one acquainted with the kelps only through the more widely distributed genera such as Laminaria and Alaria, Egregia must always be the most interesting of the family. Algologists agree in assigning to this plant the high-

FIG. 27. Lessoniopsis (hanging) and Postelsia (upright) growing on an overhanging shelf exposed to the heaviest surf. Lessoniopsis is about two meters long and Postelsia, one half meter.

est place among the kelps as being the most specialized of them all. It is a genus of the western coast, represented by two species, one northern, the other southern. Both are extremely variable and in their many forms and intergradations present to the taxonomist a problem of more than usual difficulty. Some features of the morphology of the northern species, *Egregia menziesii*, have been presented in a paper by Ramaley ('03), illustrated with some excellent figures of adult and middle-aged plants, while Reinke ('03) has also given figures and a brief description of somewhat younger plants. The development of this species which grows abundantly at the Minnesota Seaside Station, will be worth considering in detail in connection with the other kelps discussed above because of its greater complexity.

Egregia, like Nereocystis, has an extremely long stipe; indeed, in proportion to its lamina its stipe is much longer, but its character is totally different from that of Nereocystis. In the latter plant the stipe stretches from the holdfast, frequently attached to a depth of twenty or

thirty feet, like an anchor rope, to the surface, where it holds the large float and laminæ against the impact of the heavy surf. This stipe is often less than one centimeter in thickness for half its length, but of such surprising strength that the native fishermen tie their boats to these ready-made anchors and ride out a storm, as noted by MacMillan ('99). The stipe of Egregia, however, while slender and flexible, is not bare, but covered with very numerous short proliferations along its whole length giving it the appearance of a feather boa. Some of these are photosynthetic areas, some sporophylls, some floats filled with air. The presence of such organs as air vesicles so near the holdfast shows clearly the plant's adaptation to a shallow-water habitat. It grows attached to rocks which are never deeply submerged and are uncovered even by a moderately low tide, where its branches, buoyed up by their innumerable pneumatocysts, float with their whole lengths on the surface of the water. To the boatmen along that shore a thick bed of Nereocystis is a sure sign of deep water, but a bunch of Egregia as surely marks a rock to be avoided.

The youngest plants of Egregia are extremely difficult to separate from those of Hedophyllum. The juvenile forms of both these kelps are dark brown, distinguished from most others of their size by shorter stipes, together with a rather strong development of hapteres. The youngest plant of Egregia found (Fig. 28) was 25 mm. long, with a lamina about 20 mm. long and 10 mm. wide. The holdfast had already developed a circle of secondary hapteres, although the primitive holdfast could be made out beneath the secondary. The stipe was but 3 mm. long, cylindrical, and featureless except for a very slight thickening about a millimeter below the base of the blade. This appeared to be the beginning of the proliferations which characterize the later stages of the plant.

The thickening of the stipe soon becomes more pronounced and develops into a pair of horns about a millimeter long just below the base of the lamina and lying in the same plane (Fig. 29). These are the only dis-

FIGS. 28–31. Egregia. Five sixtns natural size.

FIG. 28. Youngest plant, barely distinguishable from Hedophyllum at this age, cf. Fig. 37, which is less eroded.

FIG. 29. Plant showing the first pair of proliferations on the stipe.

FIG. 30. Plant with the transition region roughened by many capillary proliferations, tuberculate ridges appearing in the base of the lamina.

FIG. 31. Base of a much older plant showing the differentiation of the first branch (*b*) made evident by the appearance of proliferations on its stipe, first pneumatocyst (*p*) just appearing, base of stipe remaining smooth.

FIGS. 32–34. Egregia. One half natural size.

FIG. 32. Whole of the plant shown in Fig. 31, proliferations on the lamina absent at the tip, but well developed below.

FIG. 33. Much younger plant than Fig. 32, capillary proliferations prominent in the transition region, laminar proliferations just beginning to appear on margin of both stipe and lamina, tip of lamina smooth, other portions covered with protective ridges.

FIG. 34. Older plant in which the lamina has reached its maximum development and the stipe has begun to grow, several well-developed pneumatocysts and young branches are evident among the outgrowths from the stipe.

tinguishing features of the plant until it reaches a length of about 40 mm. In plants of about this length a few round tubercles begin to appear at the base of the lamina, which has hitherto been smooth as in Hedophyllum. A specimen 75 mm. long (Fig. 30) showed numerous tubercles in the transition region, giving it a roughened appearance; and there were three instead of two horns below the zone of the tubercles. The basal portion of the stipe was still smooth as in the youngest specimen. In this plant the stipe had elongated scarcely at all and the growth had been restricted to the lamina, which extended through 70 of the 75 mm. of the plant's length. Tubercles similar to those of the transition region had also appeared and these were shown by transmitted light to be connected with streaks of denser tissue running lengthwise through the lamina.

After this stage, as in Lessoniopsis there is some variation in the age at which the various structures appear. A specimen 18 cm. long (Fig. 33) will serve as an illustration of the next step. Here the streaks beneath the tubercles of the lamina had become prominent ridges, much larger than the small tubercles at their summits. The ridges stood out so strongly as to cause depressions on the opposite side of the lamina beneath them. This gave the lamina a wrinked appearance and added greatly to its strength. The margin was entire or slightly undulate, but at the base were a few short serrations which looked much like the tubercles of the stipe. The roughened region of the stipe was about 1 cm. in length and no longer terete like the lower smooth portion, but somewhat flattened. In place of the horns of the younger specimens were several outgrowths, the largest of which bore a small orbicular lamina. The holdfast had become nearly 2 cm. in diameter by the great elongation of a few hapteres.

In view of the proportions assumed by the adult plant the relation between the lamina and stipe in the juvenile forms is most interesting. In the smallest specimen the lamina is only about three times as long as the stipe.

But further growth is for a time almost restricted to the lamina until the ratio is increased to ten or fifteen to one. After this stage the stipe begins to grow and soon surpasses the lamina, which seldom exceeds half a meter in length, while the stipe sometimes becomes fifteen or twenty times as long.

A specimen 12 cm. in length (Fig. 32) though only two thirds as long as the one just described, was considerably more advanced. The uppermost quarter of the lamina was entire, as in the last plant, and below the tip were a few serrations like those at the extreme base of the former. Toward the growing point these outgrowths were larger and had become spatulate proliferations about a centimeter long, fringing the basal two thirds of the blade. The stipe had reached a length of 3 cm. Its numerous tubercles were much elongated and frequently dichotomously branched, once or even twice giving the peculiar roughened appearance characteristic of the adult. The proliferations along the lateral edges of the stipe were much more numerous than in the former specimen; some of them were simple laminar appendages; others were inflated into small globular pneumatocysts (Fig. 31, *p*); on others the stalks were roughened by small tubercles like those of the main stipe. Some of these last, if detached, might easily pass for young plants cut off just above the holdfast.

Though marked changes are yet to occur before the plant becomes mature, they may be understood by a comparison of the adult with this young plant (Fig. 32). The most conspicuous change is of course the great elongation. While this is especially noticeable in the stipe, the lamina likewise grows until it reaches a length of about 50 cm., but its width increases scarcely at all, seldom exceeding 4 cm. The proliferations from this narrow lamina become so numerous that they completely mask the distinction between it and the stipe, and it is only by close inspection that the lamina may be recognized. The growth of the stipe carries the lamina far away from the holdfast, where it is exposed to the severest action of the

waves, which lash the plant until the lamina together with the meristem is torn off and there remain simply the stipe and holdfast.

The stipe remains smooth for a few centimeters above the large branching holdfast, this being evidently a persistence of the smooth basal region of the young plant. Some of the lower tubercles, however, disappear, so that the smooth area now extends farther from the base than originally. This portion is terete, but at a length of about a decimeter the stipe becomes flat and strap-like about four times as wide as thick.

In the younger specimens the proliferations from the stipe and lamina are all small and not very numerous. In the adult they enlarge very greatly and increase in numbers so as to become by far the most conspicuous feature of the plant. The increase, both in number and size, is most marked toward the growing point, those at the base generally remaining small and scattered. Farther out along the stipe they are found of all lengths up to about 12 cm. and of various forms, as figured by Ramaley. They stand as thickly as possible along the stipe; in some places by actual count upwards of a hundred were found in a single centimeter of its length. Of these only a few were large and more than half less than a centimeter long. Crowded as they are along the edges of the stipe, they never arise from its faces, which are bare except for the tubercles described above. The air vesicles are formed at frequent intervals, providing sufficient buoyancy to keep the plant floating just beneath the surface with the tips of the proliferations emerging. When mature, they are about 30 mm. long, with an average capacity of about one cubic centimeter. Others of the outgrowths remain permanently small and become sporophylls. The outgrowths on the lamina also increase in size and number, but become neither so large nor so numerous as on the stipe. As noticed by Ramaley, no bladders nor sporophylls develop on the lamina.

Egregia becomes much branched before it is mature. Although Ramaley suggests that the branching may have

FIG. 35. Egregia, base of small plant with the characters of the adult except for the small number of branches, though only a few of those present could be shown, while the others were piled up in a mass to the left of the holdfast, (*a*) a dwarfed branch with a frilled margin. One fourth natural size.

an appearance similar to Lessonia, it is brought about by a fundamentally different process, as has already been noted by Setchell ('93) and by Reinke ('03), who figure several stages in the development of a branch. Some of the earlier proliferations, as stated above, soon develop roughenings on their stalks like those of the main stipe and take on the appearance of younger specimens of the species (Fig. 31, *b*). This is the first external indication of an important difference in the constitution of these outgrowths from the ordinary proliferations. For in them has become differentiated a meristem independent of that of the primary branch. They develop exactly as did the main axis and soon become indistinguishable from it except in the manner of attachment to the holdfast, possessing all the structures which have been described for a primary branch including other branches which in turn go through the same process. After several such branches have been formed there is a modification of the process. The laminæ are dwarfed, while their margins become conspicuously puckered and ruffled (Fig. 35, *a*). Sometimes the ruffles are so pronounced as to completely enfold the meristem. In such a branch proliferations from the lamina appear very late, but the ruffle gives it a similar aspect. The dwarfed condition of the lamina persists until the stipes become several centimeters in length, when the usual relations of stipe and lamina become manifest. Though roughening may appear on other parts of the plant, the development of meristematic proliferations is confined to the basal portion; branches do not develop at a distance much exceeding 20 cm. from the holdfast. Around the base of any old plant there is always a large number of short branches in all stages of development, but there are not often more than a dozen long branches at any one time. The general appearance of the numerous dwarf branches suggests that they may not have a rapid development like the first branches, but rather grow very slowly or lie dormant for a time like the dormant buds of trees.

This method of branching is peculiar to Egregia and, as

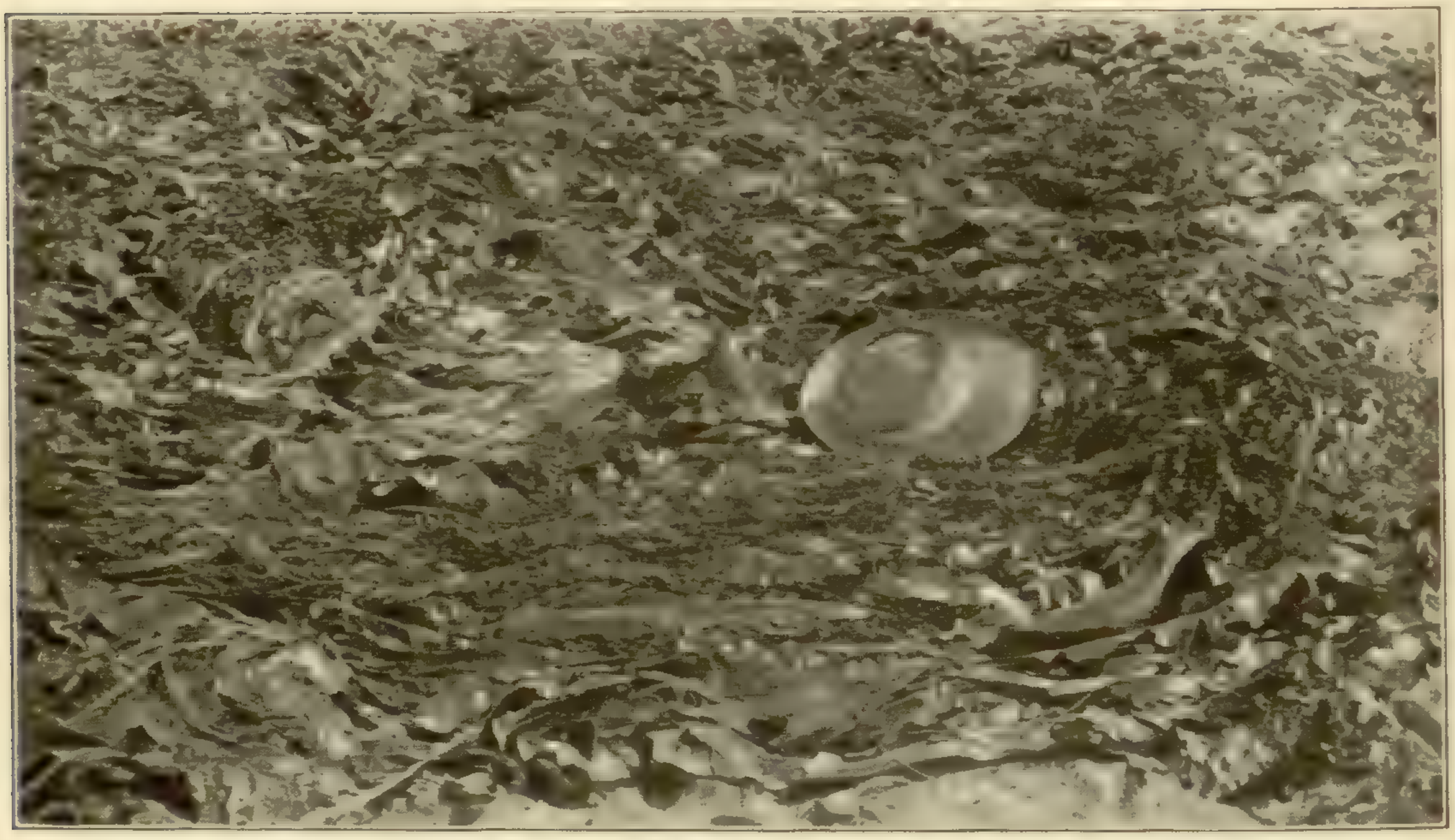


FIG. 36. Egregia growing in a thick bed of kelp in which are prominent Alaria (with a midrib) and Hedophyllum (in foreground, especially at right).

far as the writer knows, nothing like it occurs in other kelps save in Thallasiophyllum. It is a matter of great interest from several points of view. Morphologically it gives the best reason for considering Egregia the highest of the Alariatæ, although that position would probably be accorded it without question because of the differentiation of the ordinary proliferations alone. The other members of this subfamily produce outgrowths which function as sporophylls, and in some of them, *e. g.*, Eisenia, these become the main photosynthetic areas of the plant. The development of meristems in such outgrowths, leading to the formation of branches, is the next step towards greater complexity and the logical summit of the Alaria series. But its greatest interest is from the ecological point of view. The extreme length of the stipe pushes the growing point far out, where it is lashed severely by the waves and frequently destroyed. Were the plant dependent on this for its continued healthy existence, as in Laminaria, it might easily be killed or at least handicapped for a considerable part of the time by the loss of the blade until a new one could be regenerated, as in many species of Laminaria. But, should the older branches be injured, these basal branches may develop at any time. By their

presence the plant is practically possessed of a new basal meristem supplementing and to a certain extent supplanting the primary meristem. Once established in a favorable situation, a plant may therefore maintain itself indefinitely, casting off old branches and developing new ones continuously.

D. *Hedophyllum*

Because of the close similarity of the young stages of Egregia and *Hedophyllum sessile* it will be of interest to add a short description of the latter. It has already been the subect of considerable study by Setchell, who has published ('05) a discussion of its development well illustrated by figures. His paper, however, was written from another point of view than the present, namely, the relationships of *Hedophyllum sessile* to the other species of Hedophyllum and to Agarum and Thalassiophyllum. Since from this standpoint the very young forms of Hedophyllum are not important, Setchell was not particular to obtain plants less than about 5 cm. in length. But for a comparison with Egregia the younger forms are of the most interest. This species[2] is extremely abundant at the Minnesota Seaside Station, outnumbering in individuals any other kelp present on that coast. It grows at the highest level occupied by the kelps, and in various situations as regards wave action.

Very young plants of Hedophyllum are difficult to distinguish with any certainty from Egregia and from the various species of Laminaria growing in the same locality. Hedophyllum is, however, much more abundant in adults and juvenile forms, and as the specimens selected were taken from beds composed mostly of Hedophyllum, the probabilities are greatly in favor of a correct determination. The youngest plant (Fig. 5) measured approxi-

[2] Though Puget Sound is given as the southern limit of the other American species, *Hedophyllum subsessile*, I have been unable to satisfy myself of its occurrence at Port Renfrew. Two distinct series of juvenile forms are, however, represented there, one with a narrow blade like those which Setchell figures, and, as here described, another with a very broad, cordate blade even when very young. What the relations of these may be to the adult plant I have not yet fully determined.

FIGS. 37–42. Hedophyllum, series of young plants showing the gradual obliteration of the stipe by the broadening of the transition region, and the origin of new hapteres higher and higher up the stipe. Four fifths natural size.

mately 2.3 mm. in length and the margin of the primitive disc was nearly smooth. The edge of the lamina was only one cell in thickness, but there were evidently several layers in the middle region and toward the base. In a specimen 6.5 mm. long the holdfast had become distinctly crenate around the edges and the one-layered lamina had disappeared. The crenations had become much more pronounced and had assumed the characters of primary hapteres in a specimen 10 mm. long (Fig. 6).

By the time the plant reaches the length of an inch its determination is not difficult. A specimen 28 mm. long (Fig. 37) will serve for comparison with the youngest Egregia described. The lamina is narrower and longer than in that plant; the holdfast has not as yet developed secondary hapteres and the stipe is shorter. Though the stipe always remains short, it usually becomes longer than is shown in this plant (about 5 mm.). The narrowness of the lamina is characteristic, but is not sufficiently marked at stages earlier than this to render diagnosis easy.

Soon after this stage secondary hapteres begin to appear above the primitive holdfast. Though they arise in circles as in the other kelps, they usually develop quite unevenly in the young plant, some members of the circle becoming long, while others are yet mere knots on the stipe. When a length of about 8 cm. is reached the stipe begins to thicken and flatten. The transition region, which has been sharply marked off, becomes less and less distinct and the plant comes to consist of a lamina with a cuneate base anchored by the holdfast (Fig. 42). This condition sometimes persists until the plant has reached a considerable size. More usually, however, the broadening continues and quickly brings about the adult condition.

When mature (Fig. 43), *Hedophyllum sessile* becomes a broad, cordate, sessile plant anchored by a mass of hapteres at its base. Its lamina is torn to ribbons like a digitate Laminaria, so that it may resemble one of the kelps with true branching. The hapteres arise in circles one above the other higher and higher up on the stipe

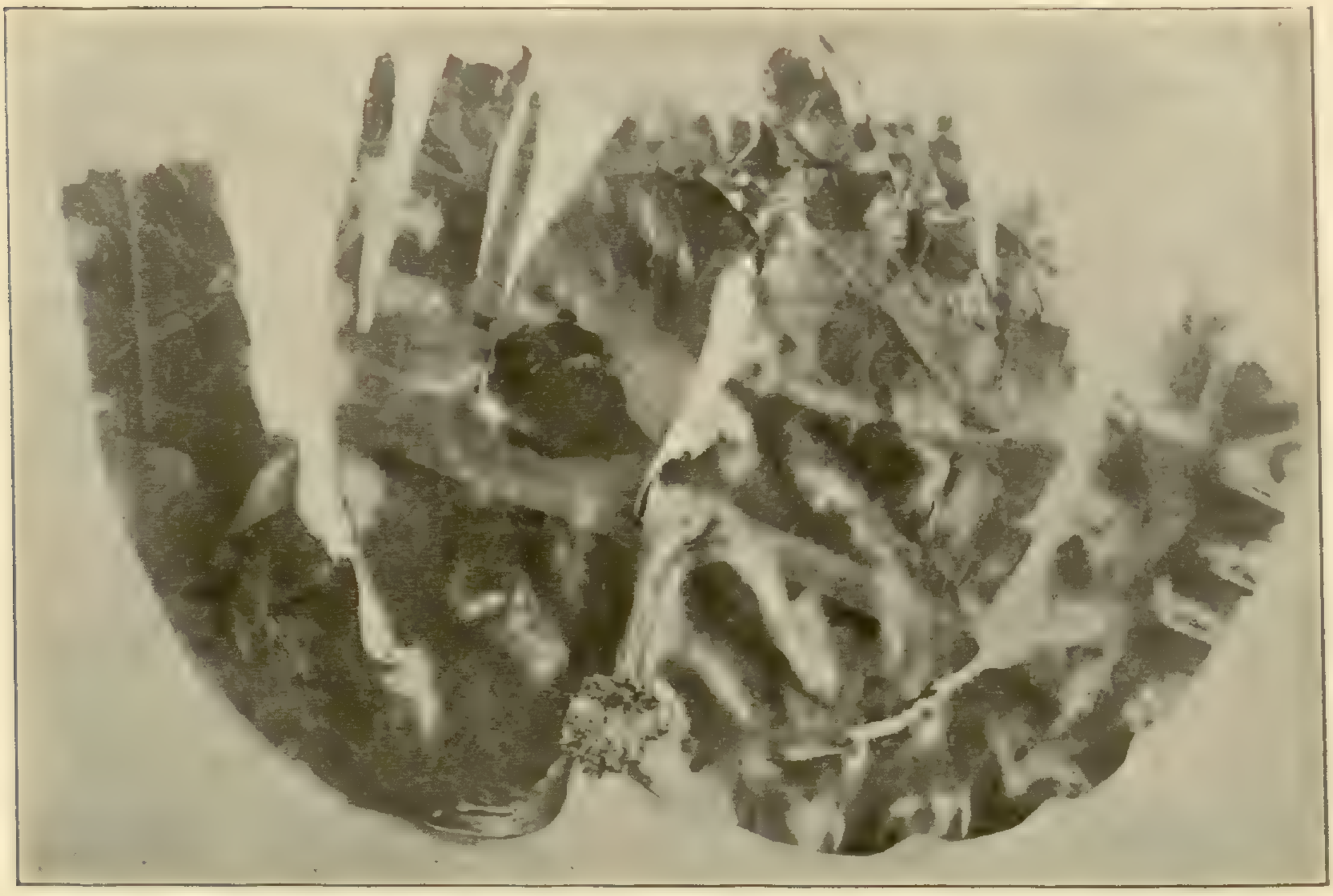


FIG. 43. Hedopnyllum, medium-sized plant showing the cordate lamina torn by the waves. A fully mature specimen would be a rosette so dense that its structural relations could not be made out. One fifth natural size.

until they obliterate it and even come to grow out from the lamina itself. Thus there arises a thickened basal portion of the lamina which forms a conical holdfast, as in the other kelps, while new circles of hapteres may be seen on its upper edge, growing out from the undifferentiated lamina. By this process the holdfast region extends beyond the bases of the segments of the lamina so as to give the old plant the appearance, not of one, but of several independent laminæ springing from a common holdfast. Considering the similarity of the young plants to Egregia, the divergence of the adults is very striking.

(*To be concluded*)

THE LARVA AND SPAT OF THE CANADIAN OYSTER

J. STAFFORD, M.A., PH.D.

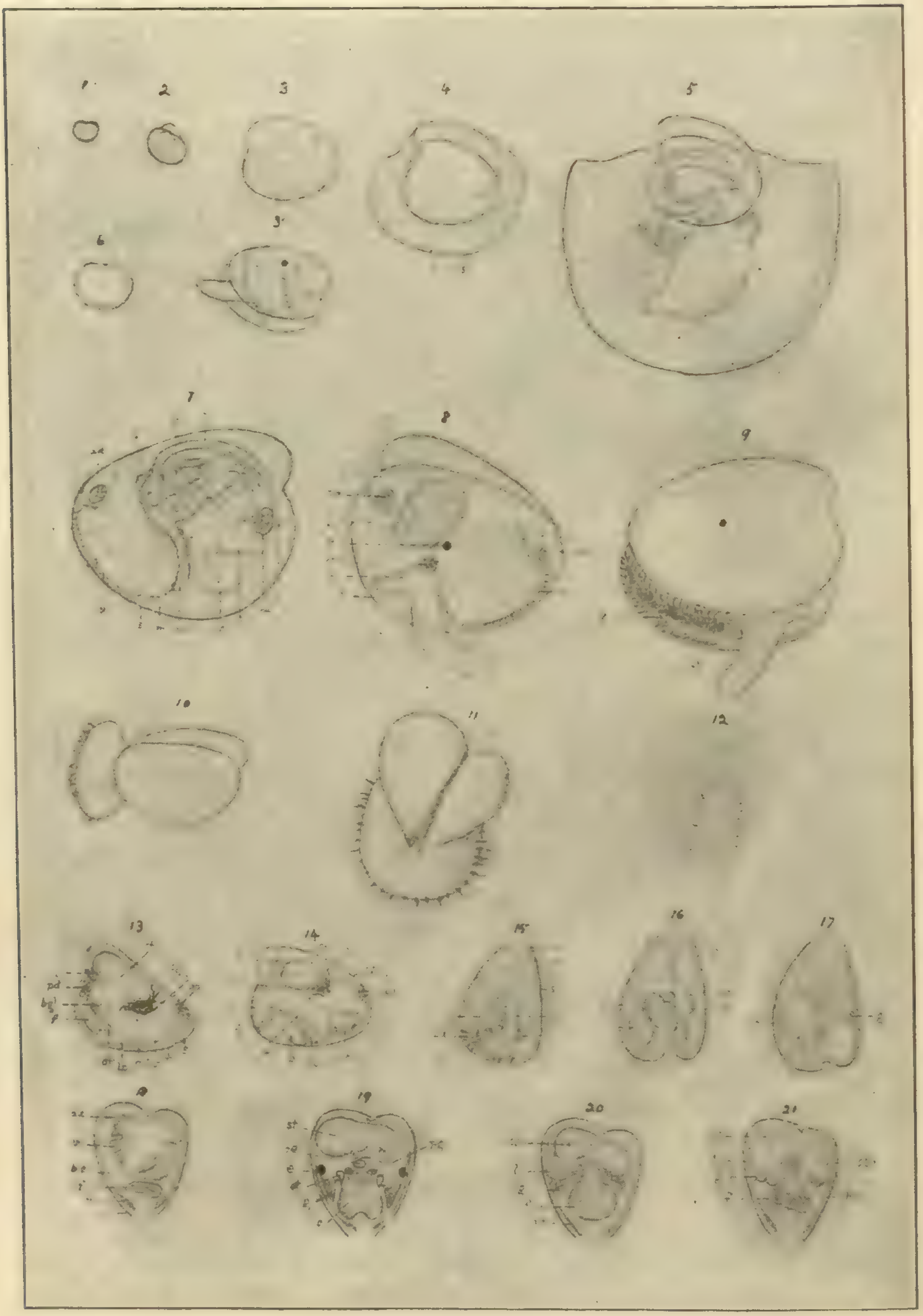
MONTREAL

I. THE LARVA

IN the summer of 1904, at Malpeque, Prince Edward Island, on behalf of the Canadian Marine Biological Station, I undertook to gather what information I could upon the life of the oyster from the time it becomes a distinct bivalve veliger to the time when it is recognizable by every oyster fisherman as a spat oyster.

Brooks, of Johns Hopkins University, Baltimore, to whom belongs the immortal glory of having discovered that American oysters are unisexual and that artificial fertilization of the eggs and rearing of the larvæ are possible, had worked out the spawning, fertilization, segmentation, gastrulation and organization up to the earliest microscopic free-swimming bivalve veliger, and there was no lack of literature on oyster culture beginning with macroscopic oyster spat of, let us say, the size of one's thumb-nail. But the intermediate stages, mostly microscopic, seemed to be scarcely, if at all, known, and there were many questions as to the time and place where they might be found as well as to their anatomy and comparison with other genera which required investigation.

The possibility of raising young oysters from eggs and keeping them alive without admixture with other individuals or other species until one had seen the whole series of continuous transformations into the adult seemed next to impossible. I chose rather to learn to recognize the larval oyster in plankton collections, a method which had apparently received no attention. I



EXPLANATION OF PLATE

a, anus; *ad*, anterior adductor muscle; *bc*, branchial chamber; *bgl*, byssus gland; *c*, chitin; *c*, eye spot; *f*, foot; *g*, gills; *h*, heel of foot; *i*, intestine; *l*, liver; *lp*, lower lip; *m*, mantle; *mo*, mouth; *oc*, œsophagus; *og*, supra-œsophageal ganglion; *ot*, otocyst; *pd*, posterior adductor muscle; *pg*, pedal ganglion; *s*, larval shell (prodissoconch); *s'*, spat shell (dissoconch, nepionic); *sbc*, supra-branchial chamber; *st*, stomach; *v*, velum.

FIGS. 1, 2, 3, 4, 5. Development of Canadian oyster from bivalve veliger to young spat. From the right side, drawn under the same conditions throughout, Leitz microscope, oc. 3, obj. 2 (revolver). Zeiss Zeichenapparat. Drawing desk flush with stage and slanting upwards at proper angle to prevent distortion.

Measured under Leitz oc. 5 and obj. 4 with a Leitz oc. microm. valued by a Leitz stage microm.

FIG. 1. Oyster larva, young straight hinge stage. .089 mm. high, .103 mm. long.
" 2. Oyster larva, early umbo stage. .138 × .144 mm.
" 3. Oyster larva, full grown. .31 × .34 mm. Fig. 3' from the left side.
" 4. Oyster spat, with the valves of the larval shell (prodissoconch) plainly retained. .51 × .55 mm.
" 5. Oyster spat. .876 × 1.030 mm. The larval shell is .369 × .384 mm.
" 6. Same as Fig. 1 drawn under oc. 3, obj. 4, for comparison with Figs. 7, 8, 9.

FIGS. 7, 8, 9. Same as Fig. 3 drawn under oc. 3, obj. 4.

FIG. 7. Oyster larva from the left, with several organs sketched in.
" 8. Same from the right, with dorsal hinge-line tilted towards the observer.
" 9. Same from the left, with ventral gaping margin tilted towards the observer.

FIGS. 10, 11, 12. Free-hand drawings of full-grown living oyster larvæ, not so highly magnified as Figs. 7, 8, 9.

FIG. 10. Oyster larva, full-grown, from the left, velum protruded and partly expanded.
" 11. Same from behind, attached to the slide by its fully expanded velum, large left valve.
" 12. Same from the ventral surface, velum partly protruded.

FIGS. 13, 14, 15, 16, 17, 18, 19, 20, 21. Sections of full-grown larvæ, drawn free-hand.

FIG. 13. Section median sagittal (nearly), from the right. The foot being turned sideways was not split medially.
" 14. Same of another series.
" 15. Section horizontal (upper), from above.
" 16. Same (deeper).
" 17. Same (lower).
" 18. Section frontal, transverse (anterior), from behind.
" 19. Same (median).
" 20. Same (near middle) of another series.
" 21. Same (posterior) of same series as 18 and 19.

had never seen an oyster larva or a young spat, but I had followed the main stages in the life history of the mussel.

Beginning my plankton-collecting at the end of the first week in July, it soon became apparent that there were many species of bivalve larvæ present in the water, and in order to refer these with some precision to the proper adults it would be necessary to carry on at the same time a faunistic study of the Mollusca of Richmond Bay. The commonest of these relative to my purpose were found to be species of Mytilus, Mya, Venus, Clidiophora, Ostrea, Anomia, Mactra, Modiola, Pecten, Saxicava, Macoma, Ensis, Yoldia, etc., and to find larvæ corresponding to all of them was beyond my ability. Nevertheless, several larval forms gradually became familiar and I referred them provisionally to certain adults. On the twenty-fifth of July what I took for oyster larvæ (Plate, Fig. 3) first decidedly claimed my attention and as time went on I became more and more convinced of the correctness of my surmises. But belief is not proof, so I set to work experiments with a view to entrap oyster larvæ on glass plates at a time when presumably the larvæ become too heavy to swim with ease, settle towards the bottom, creep about and select some clean, solid surface upon which they fix themselves and transform into the youngest oyster spat. This was successfully accomplished on the sixteenth of August when I obtained a minute oyster spat (Fig. 5) still preserving most evident characteristics of the larva, but with the addition of a rim of spat-shell, and later I found many minute spat-oysters on various natural objects such as shells and stones.

The plankton was collected in conical nets, made of fine-meshed silk bolting cloth, attached at the broad end by a rim of linen to an iron ring one foot in diameter, to which were tied, at equal distances, three pieces of cod-line, the other ends being brought together and secured to a towing line. The small end of the net was also

furnished with a linen rim in which was tied the neck of a wide-mouthed bottle. To the towing line, in front of the net, was fastened a sinker and the whole was dragged through the sea-water, behind the little steamer *Ostrea,* under reduced speed, for about a mile, when the net was hauled up, the contained water carefully drained through one side, after which it was dipped several times right side up into the sea and raised so as to wash all the plankton material down into the bottle. The bottle could then be removed and corked, the net washed by throwing it overboard again open, and other bottles used for different places or different depths on the same excursion.

In such a manner may be procured a wealth of plankton material, but slight modifications in mode of operation may be employed, depending upon the nature and object of one's research. The older bivalve larvæ are compact, heavy, well protected, so that they will stand comparatively rough usage. By the time one reaches the laboratory the great mass of the copepods may be dead and sunk ,towards the bottom of the bottle, but underneath this mass one can see the darker, granular, more sand-like bivalves. These may be withdrawn by a glass tube and emptied into a watch glass, the more superficial, lighter things being again removed by a pipette. In this way bivalve larvæ may be obtained, sometimes by thousands, and almost entirely free from admixture with other animals, while among them, if collected at the proper time and place, will occur oyster larvæ.

At Malpeque the full-grown, free-swimming, pelagic, or more or less abyssal, or creeping larva of the oyster (Figs. 3, 7, 8, 9) possesses a characteristic brownish-red color—suggestive of the soil of its native island shores—a shade which enables it to be immediately distinguishable from every other bivalve larva with which it is associated. The shell (prodissoconch) is asymmetrical, inequivalve and inequipartite, the left valve being larger, more convex and with a large umbo, the right one smaller, flatter

and with a moderate umbo, while the umbos have a postero-dorsal position, projecting backwards and upwards and making the shell broader, deeper, squarer behind and tapering but rounded in front. The largest measure about .358 by .365 mm. in height and length, but, owing to the different convexities of the valves, the greater breadth above and behind, and the different degrees to which it may be tilted in this way or that, the same larva may vary much in apparent size and shape according as to how it is presented to the observer. The following are measurements of half a dozen larvæ at different ages selected from a large number of records: .131 x .138 mm., .138 x .144 mm., .207 x .241 mm., .241 x .276 mm., .296 x .345 mm., .345 x .372 mm. The larval shell of the young spat (Fig. 5) measures .369 x .384 mm. and may be taken to represent the maximum size.

When mounted on a slide the larvæ are accustomed to remain quiescent, and from their deep coloration are difficult to examine, but sometimes a more transparent one permits certain organs to be traced. When freshly collected and examined in a watch-glass of pure, cool water from their native habitat, many of them exhibit the greatest activity, swimming hither and thither or circling round and round by means of the velum (Figs. 9, 10, 11, 12), a swimming organ which they protrude between the antero-ventral margins of the shell-valves and expand in a manner resembling the opening of an umbrella. The margin of this is densely covered with large cilia, the violent flapping of which propels the animal forwards with the heavy body and shell suspended beneath the velum. Jarring the watch-glass will cause the animal to immediately withdraw its velum (Figs. 7, 8), at the same time snapping the valves of its shell together and dropping towards the bottom. Such observations illustrate the ordinary mode of locomotion and the response to violent movements in the sea, for during heavy gales a plankton net will take few or no larvæ near the surface.

An organ of immense interest to zoologists and of vast

importance to the animal is the foot (Figs. 7, 8, 9), a structure which I claim the privilege of having first recognized. The adult oyster is normally a quiescent, sessile animal, having its left valve solidly cemented to a rock or another shell. Under these conditions a creeping foot, such as is possessed by a clam, a mussel, or a quohog, would be of no service to the oyster, which in fact has none. Influenced, no doubt, by this difference in the adults, zoologists have been accustomed to think of the oyster larva as being vastly different from other bivalve larvæ, and repeatedly state that it has no foot, a misconception which justifies the view with which I started out, viz., that plankton stages of oyster larvæ have been neglected, embryologists jumping from early veliger or phylembryo to late prodissoconch or early nepionic periods. The foot, at the period we are studying, is well developed, and is a most capable organ, by means of which the animal can creep rapidly about and forcibly flop its heavy shell from one side to the other. When extended it is a long, slim, ciliated, muscular outgrowth from the middle of the ventral surface of the body of the larva, behind the velum. Its lower or posterior surface sometimes appears flattened or even grooved lengthwise (Figs. 18, 19, 21), and at a short distance from the base of attachment there is a heel-like projection (Figs. 8, 9, 13, 14, 21) which doubtless contains the opening of the byssus gland. When quiescent the foot is shortened, retracted and closely tucked away behind the velum and between the gills, but it can stretch so far as to perform feeling movements over all parts of the body within the shell and even bend up along the outside of the shell. I have no doubt that at the end of the free-swimming period, when the velum fails as an organ of locomotion and the larva has to remain at the bottom, the foot then proves to be of greatest service in freeing the little animal from overwhelming sediment, creeping on to a solid substratum, clearing a suitable place for fixation, and perhaps furnishing a transitory byssus.

Lying against the inner sides of the shell-valves are right and left folds of the mantle (Figs. 7, 18, etc.), the free edges of which secrete the shell material and may, like velum and foot, at times protrude beyond the margin.

Along each side underneath the mantle, past the base of attachment of the foot to the body, lie the gills (Figs. 7, 8, 9, 19, 20, 21), extending backwards and downwards to near the posterior edge of the shell; in the oldest free-swimming larva there are about eight filaments in each series, diminishing in size from before backwards, the last ones being mere knobs; their lower ends are free, but their upper ends spring from one continuous fold that, behind the foot, joins its mate of the opposite side, near the margins of the mantle. They correspond to the right and left inner gills of the adult oyster.

The alimentary canal (Fig. 7) is much longer than the body and in consequence has become folded, the greater part lying to the left (Figs. 17, 19, 20) of the median sagittal plane, but mouth, œsophagus and anus are median. The mouth (Figs. 7, 13) is a funnel-shaped opening lying immediately below and behind the velum, to which its walls are attached and with which it is protruded and withdrawn, so that it can only be functional while the velum is to some extent expanded, when the activity of its cilia may also contribute to the process of feeding. The œsophagus (Figs. 7, 13, 14, 19) lies between velum and foot in the median sagittal plane as well as in or very near the median transverse plane of the body. Here it passes dorsalwards, between the first gill-filamets, and opens into the stomach with its large brown lateral liver-sacs. The intestine passes backwards towards the right and then forwards towards the left, when it again turns backwards and upwards in the left umbo and finally downwards in the median plane over the posterior adductor muscle.

In front and above the velum is an anterior adductor-muscle (Figs. 7, 13, 18, etc.), running transversely between the valves, while below the posterior parts of the

umbo is a larger, transverse posterior adductor muscle (Figs. 7, 13, 21, etc.). Retractor fibers converge from the velum to points in the umbos and there are intrinsic muscle fibers in the velum, the foot and the mantle.

About the center of the animal, as viewed from one side, and anterior to the gills are two conspicuous, black pigment spots (eye specks, Figs. 3, 8, 9, 19) that, in transverse sections of the larvæ, are found to be situated right and left on the lateral walls of the body, just in front of where their ectoderm becomes continuous on to the outer surface of the first gill filament.

Immediately behind and below the pigment spots, but on a deeper level, are right and left otocysts (Figs. 8, 9, 16, 19), each containing about a dozen otoconia. Sections show them to be placed laterally in the proximal part of the foot, close to where its ectoderm passes over on to the inner surfaces of the first gill-filaments. Between the otocysts, and of course behind the œsophagus, are the two connected pedal-ganglia (Fig. 19), and at the center of the base of the velum, in front of where the œsophagus joins the stomach, is the supra-œsophageal ganglionic mass (Figs. 13, 14), protected in front by what appears to be a yellowish-brown, flexible, chitinous layer which gives origin to the muscle-fibers of the velum.

Transverse, sagittal, and horizontal sections (Figs. 13–21) of oyster larvæ, prepared in the usual way by decalcifying the shells, staining in alum-cochineal, embedding in paraffin, sectioning with a Yung microtome, and mounting on a slide in Canada balsam, have contributed much towards an accurate understanding of the relative positions of the organs.

Development naturally begins with small, simple eggs and proceeds to larger and more complex larvæ. By the time I had become oriented with regard to the latter and proved to myself that they can actually metamorphose into oyster spat it was of course too late for that season to obtain and follow the growth of the youngest larvæ. Examination of preserved plankton collections, however,

although far from being as satisfactory as fresh, living material, shows oyster larvæ (Figs. 1, 6) but little older than the stages at which the observations of Brooks closed, viz., six days old from the date of fertilization. Brooks did not give measurements, so that it is impossible to be exact on this point—I can only judge from the shape and organization. Plankton collected July 11, 1904, between Curtain Island and Ram Island contains an abundance of minute, transparent bivalve larvæ (phylembryos) in what may be known as the straight-hinge stage to distinguish them from the older larvæ with high umbos (the umbo stage) that obscure and modify the hinge line. A hasty and superficial observation of these combined with the fact of their occurrence in proximity to oyster beds might easily lead to the conclusion that they are all oyster larvæ. But they are not. Many of them are clams, a few are mussels, and one in a great number is an oyster. A full statement of how I have determined this would require too great a digression and will be dealt with in another paper, but it results from a comparative study of bivalve larvæ in the different localities of the Biological Station combined with researches into the distribution of adult forms. Adults of the above-mentioned genera are easily distinguished; the full-grown larvæ less easily, for, since they bear little resemblance to the corresponding adults, other marks of distinction have to be selected; but the young larvæ are still more difficult, for, according to the biogenetic law, the younger they are the more nearly they resemble some stage of the common original ancestor and of course approach one another in likeness. Under such conditions the practicable, distinguishable characters may again be different and require a more critical scrutiny. Since I first turned my attention to bivalve larvæ I have found it necessary to change my point of view and mode of procedure. One can not safely trust to the eye in judging proportions, but must resort to a definite and unvarying method of measuring by means of ocular and stage micrometers.

For each of the commonest species a table of lengths was prepared, jumping only one of the smallest units of my ocular micrometer at a time, and the heights were filled in as individuals of these lengths occurred. Thus larvæ of the mussel, the clam and the oyster, at the period we are considering, measure as follows:

	Length.	Height.	Length of hinge-line.
Mussel	15	10	11
Clam	15	13	10
Oyster	15	13	7

—a table which will immediately make apparent the truth of many of my statements. The eye can easily perceive a difference in the proportions of the mussel and the clam, but it requires a certain refinement of judgment to do the same for a clam and an oyster. Such an oyster larva actually measures .103 x .089 mm. in length and height, and has a short, slightly concave hinge-line of scarcely half the length of the shell.

I have said that in collections of straight-hinge larvæ but one in a great many is an oyster. A similar statement might be made for any period in the larval existence of the oyster. Upon one occasion when the umbo-stage was most abundant I estimated that there was only one oyster among twenty-five bivalve larvæ. Another time I found that when the plankton net was towed at the surface against a wind it caught about a quarter as many oysters as in going back over the same distance with the net sunk a few feet below the surface of the water.

I am of opinion that the study of plankton collections for bivalve larvæ will be found a most useful help in determining the breeding season—that is to say the height of the breeding season. From the foregoing pages it may be concluded that oyster larvæ are present in the water from the eleventh of July to the first September, and that oyster spat are present from the sixteenth of August. This would seem to indicate that the second half of August is taken up with the last stages of growth of late larvæ and that the period of growth of the masses

falls between July eleventh and August sixteenth. Taking it that the youngest larvæ I have described are little older than those of similar shape and structure described by Brooks, and allowing a possible retardation on account of the climate, we should conclude that the eggs were deposited pretty close to the first of July. That spawning does not take place much before this I judge from the fact that in 1905, while I was at Malpeque preparing the station for removal, I took plankton at intervals between June seventh and twenty-sixth and this shows no oysters and but few mussels and clams.

In the microscopic examination of the genital organs for the purpose of determining the time of sexual maturity, unless one examines a very great number taken from many different localities, he may light upon an abnormal number of individuals that are immature or that have already spawned and so form a wrong conception as to the period of maximum spawning. Combination of both methods should give the best possible results.

I have purposely attempted to disregard the statements of others in order to be entirely unbiased as to my results, and from the facts of my own observations I am disposed to think that the period of maximum spawning falls in July, but that a few may spawn earlier and a greater number may straggle in later.

It is a matter of regret to me that it did not fall to my lot to begin the study of oyster larvæ during the first summer at Malpeque, for then I could have used the second summer to verify, fill in details, and follow out suggestions. I have looked forward ever since for an opportunity to do so, and this is my chief excuse for the delay in publishing these results.

Chief points of importance resulting from the foregoing work are:

1. Larval oysters are present suspended in the water of Richmond Bay, Prince Edward Island, in July and August.

2. They may be taken in a plankton net at the surface and at various depths.

3. All stages from the freshly fertilized egg to the full-grown larva must be there.

4. The free-swimming period is, perhaps, considerable, close on a month.

5. They feed and grow, while in the free-swimming state, through a straight-hinge to an umbo-stage.

6. Normal fixation takes place when the larval shell is about .38 m. in length, and then the spat period begins.

7. A metamorphosis occurs through loss of larval organs as velum, foot, eye-spot, otocysts, etc., and a development of new organs as spat-shell, additional gills, palps, etc., is begun.

8. The larval shell is asymmetrical, as is also to some extent the contained body.

9. A foot, homologous with that of mollusks in general, is present in the older larvæ.

10. The otocysts contain otoconia.

11. Pedal ganglia are present.

12. A byssus-gland is present.

13. Gills are present.

14. Eye-spots are present.

15. A rigid system of measurements has been used, and a comparison of actual sizes at different periods of growth introduced.

16. Numerous niceties of structure, shape, color, activity, time, place, etc., are noted.

17. The spawning period has been limited.

18. Attention is directed to the importance of these theses and observations as bearing upon problems and methods of oyster culture.

Literature

European works referring to the development of the oyster larva are those of:

1. 1854. Lacaze-Duthiers. Mém. sur le dévelop. des Acéphales Lamellibr. *Comptes Rendus heb. des Séances de l'Acad. des Sciences*, Paris, XXXIX, pp. 102-106. Nouvelles observ. sur le dévelop. des huîtres. Same vol., pp. 1197–1200.

2. 1882 ('83). Horst. A Contrib. to our Knowl. of the Develop. of the

Oyster (*Ostrea edulis* L.). Bull. U. S. Fish Com., II, pp. 159–167, 12 figs.

3. 1884 ('86). Horst. The Develop. of the Oyster (*Ostrea edulis* L.). Rep. U. S. Fish Com., pp. 891–910, Pls. I and II.
4. 1883. Huxley. Oysters and the Oyster Question. *Eng. Illus. Mag.*, Oct. and Nov., pp. 47–55, 112–121.

American work must be considered to have originated with Brooks, whose discoveries inspired investigators at home and abroad and pointed the way to possibilities and methods of culture that were ably carried forward by Ryder, Winslow, Rice and others. Of the many papers, reprints, summaries, etc., published by Brooks I mention but one:

5. 1880. Brooks. Development of the American Oyster. Rep. of the Com. of Fish. of Maryland, pp. 1–18, 10 pls.
6. 1882 ('83). Ryder. On the Mode of Fixation of the Fry of the Oyster. Bull. U. S. Fish Com., II, pp. 383–387, 9 figs.
7. 1882–83 ('84). Ryder. A Sketch of the Life-history of the Oyster. 4th Ann. Rep. of the U. S. Geol. Surv., pp. 317–333, pls. 73–82.
8. 1882 ('84). Ryder. The Metamorphosis and Post-larval Stages of Development of the Oyster. Rep. U. S. Fish Com., X, pp. 779–791.
9. 1884. Ryder. A Contrib. to the Life-history of the Oyster. Fisheries and Fishery Industries of the U. S., Sec. I, pp. 711–758.
10. 1882 ('84). Winslow. Rep. of Exper. in the Artif. Prop. of Oysters. Rep. U. S. Fish Com., X, pp. 741–762.
11. 1889. Jackson. The Develop. of the Oyster with Remarks on Allied Genera. *Proc. Bos. Soc. Nat. Hist.*, XXIII, pp. 531–556, 4 pls.
12. 1890. Jackson. Phylogeny of the Pelecypoda. *Mem. Bos. Soc. Nat. Hist.*, IV, pp. 277–400.

Canada has done little towards a scientific study of oyster development. Three rather unpretentious articles are known to me.

13. 1895 ('96). Prince. Peculiarities in the Breeding of Oysters. Special Reports, Ottawa, pp. 10–13.
14. 1904. McBride. The Canadian Oyster. *The Canadian Record of Science, Montreal*, IX, July, pp. 145–156, Figs. 1–4.
15. 1905. Stafford. On the Larva and Spat of the Canadian Oyster. THE AMERICAN NATURALIST, Boston. pp. 41–44. (Preliminary to this paper.)

BRIEF NOTES AND CRITICISMS

Brooks (No. 5, p. 25, of the preceding list) says: "All my attempts to get later stages than these failed, etc." He refers to his Figs. 44 and 45 which were perhaps a little younger than my Fig. 1 and were six days old. I never could understand the claim that they might develop to this stage in twenty-four hours.

Horst (2, 165; 3, 904) was unable to get stages older than his Fig. 12, a straight-hinge shell of .16 mm., which according to Ryder (7, 791) would be equivalent to an American larva of half this length, *i. e.*, little younger than my Fig. 1. He adds: "I have also been disappointed in my attempts

to procure oysters in these phases of development by means of catching larvæ floating about in the sea.''

Ryder's papers (6, 383; 7, 328-9; 9, 727) are not easy to correlate on account of discrepancies in measurements or magnifications, age and occurrence, a misuse of the term embryo, etc. Making allowance for these, and combining his statements in the probable order in which they were written, I conclude that Ryder had seen two stages approximately of the same age as two I have figured. His Fig. 1, magnified 183 times measures 14.5 mm., which would give the larva an actual length of .08 mm. His Fig. 3, magnified 96 times, measures 29 mm. and similarly gives the young spat an actual length of .3 mm. But his were both fixed, and in fact it was this property which in Ryder's methods afforded the chance of their being observed. He appears to have believed that the larger one (C. $1/80$ in.) marked the proper stage of fixation but that under ''favorable circumstances'' larvæ of the size of the smaller might become fixed and then grow to the size, shape and structure of the larger, at which time they first become spat. Considering that he obtained the small ones but once, that they were attached in no regular position, and that the one figured was on its right side instead of on its left, it seems more probable that the fixation was of a transitory nature (as regarded by Jackson) or that it was abnormal, due to unfavorable artificial conditions and that the normal process is for the larva to remain free until it reaches the size of the prodissoconch in the umbo of the young spat shell. Ryder's view of the duration of the free-swimming period as limited to twenty-four hours comes nearer to a possibility if we remember that he doubtless had in mind this case of abnormally early fixation. A similar statement might be made with regard to the sentence ''The difference in magnitude between the oldest artificially incubated fry seen by me and that of the youngest fixed embryos which I collected is very small.'' These also agree very well with the larvæ raised by Brooks and by Horst. He never saw larvæ between these two stages in size. This represents a period during which the larvæ had to grow to nearly four times their former diameter and undergo a very great increase of organization. If the smaller stage can be raised as in Brooks's larvæ in six days the larger might require four times six days additional, making a month for the complete larval development. This time according to Brooks, Ryder and others might be reduced by very warm weather. It is just possible that too high a temperature of small isolated quantities of water may be one of the adverse conditions which have prevented larvæ from being raised beyond this stage. In nature they not only have a broader source of food supply but they can also sink into cooler water.

Winslow (10, 757) thought that the oyster larva is predisposed to fix itself very soon after segmentation and when the shell is developed to a slight extent the larvæ remain quiet in one place at the bottom. I can believe that they do not by their own efforts travel very far from the place of their origin for their locomotion is largely a circling or to-and-fro movement, but while suspended in the water they may be transported by tidal currents.

Jackson (12, 300) wrote: ''Between the stage Fig. 25 and our next stage, Pl. XXIV, Figs. 1, 2, there is a blank in the knowledge of the

development of the oyster. It has not been described in the European species, and all attempts to obtain it in our own species have failed. In artificial confinement the oyster dies at this stage.'' His Fig. 25 is Huxley's cut of a straight-hinge larva. Figs. 1, 2 of Pl. XXIV are Jackson's own youngest stage of the spat, obtained August 4, 1888, on glass put in a drain-pipe trap on a sand-bar in Buzzard's Bay. It was firmly attached by the ventral margin of the left valve and as it had been attached less than twenty-four hours the anatomy and shell must have been developed while it was a free larva. The figures measured 37 mm. and as they are magnified 120 diameters the actual length of the recently free larva, now a fixed spat, was nearly .31 mm.

Prince (13, 13) makes the statement: ''I captured many small embryo-oysters several miles from any known oyster areas,'' but as no measurements or drawings accompany the paper one can not judge of their size or age.

McBride (14, 151, 153) says: ''Judging from the size of free-swimming larvæ caught by the tow-net . . .. During the latter part of the month (August) the waters were swarming with larvæ which, from their exact agreement in shape and appearance with the larvæ of the European oyster, were doubtless the later stages of the free-swimming young of the Malpeque oyster. . . . The later larvæ which were captured by the tow-net are characterized by possessing a straight hinge to the shell. . . . Fig. 4. Late Larva of the Oyster captured by the Surface-net.'' The so-called late larvæ are in the light of my researches in reality somewhat early larvæ. Late larvæ would be more appropriately applied to the umbo-stage which doubtless was in the water at the time referred to, but was at that time unknown as a plankton organism. The statement that the waters during the latter part of August were swarming with young straight-hinge oyster-larvæ does not correspond with what I found at the same place the succeeding year. Upon examining Fig. 4 I find that it is not an oyster larva. The measurements are 83, 70, 51 mm. which if divided through by 5.53 will give 15, 12.6, 9.2 mm. as the length, height and hinge-line. Referring this to the table of comparison of a mussel, a clam and an oyster at this period, on a former page, it becomes evident that it could have been no other than the larva of the clam.

The shell of the larva was held to be perfectly symmetrical by Ryder (6, 384; 7, 329; 8, 787; 9, 727), but Jackson (11, 541; 12, 312) observed in his youngest spat that the lower left valve was larger and deeper than the upper right one.

A foot has been mentioned by Lacaze-Duthiers, Horst, Brooks and Jackson. Lacaze-Duthiers (1, 105) said: ''En avant de l'anus un appendice pen saillant simule un rudiment de pied.'' Horst (2, 162) stated that ''A foot-like prominence is developed, whereby the animal assumes some likeness to a young gastropod.'' Brooks (5, 53) wrote: ''Near the center of the ventral surface—the top of Fig. 32—there is a well-marked and constant protuberance of the body wall, which occupies the region which, in most molluscan embryos, gives rise to the foot, and which may perhaps be regarded as a rudiment of that organ.'' In the same paragraph and referring to the same figure he mentions ''the primitive digestive cavity'' and on page 68 ''the primitive digestive tract opens by a wide blastopore.''

No one would claim that the part referred to in these extracts is the same organ as I have described in very much later larvæ. Referring to Horst's 1882 Fig. 6 or 1884 Fig. 10 we observe that it is only an accidental prominence, since it is bounded below by the invagination of the blastopore and above by that of the shell-gland, and further it disappears later on as in 1882 Fig. 10 or 1884 Fig. 14. Jackson (12, 302) affirmed: "The nearest approach to a foot known in the developing oyster is that shown in Fig. 24, p. 299 (after Horst), and I discovered no traces of a foot in my youngest specimens." The best that can be said about all references to a foot at these early stages is that, by comparison with other species, they indicate the place where, at a later date, through growth and specialization, a foot as well as several other parts are formed between the mouth and the anus.

"Otocysts . . . here recorded so far as I am aware, for the first time," was written by McBride (14, 153), but a similar statement occurs in Lacaze-Duthiers of 1854 p. 1200, "Enfin j'ai vu apparaitre les-otolithes . . . quelques globules agités de mouvements . . . dont personne n'avait même constati l'existence." McBride's "Fig. 3. Larva of Oyster, six days old" shows two otocysts, and in the near, right, one is a single otolith. There is something wrong about this. The oyster has about a dozen otoconia in each otocyst, a fact which Lacaze-Duthiers was perhaps aware of when he wrote the words "quelques globules." If McBride's Fig. 3 properly represents his observations then it is not an oyster but a clam which I know to possess a single otolith in each otocyst. Clams are very abundant along the beach immediately below where the station stood at Malpeque and it is a reasonable inference that this larva was taken up in the water used. On the same page occur the words "shell-gland . . . mistaken by Brooks for the gut." This was first pointed out by Horst in 1882.

Regarding the presence of a byssus Ryder (6, 383; 7, 329; 9, 758) was doubtful. Horst (3, 907) believed that he had noticed a small byssus. Jackson (12, 303) concludes that the oyster does not have a byssus at any period.

The absence of gills as well as the mention of symmetry in the following extract is only one of the indications that Ryder's (8, 787) conception of an oyster larva was constantly associated with the straight-hinge stage of the phylembryo: "One of the most conspicuous differences between the symmetrical larva and the young spat is the absence of gills in the former and their presence in the latter . . . two gill pouches . . . outer gill pouches."

Jackson (12, 303) studied the gills of the youngest spat stage and knew them to be the right and left innermost gills of the adult. He also mentions palps but says little about them. Jackson's study of the gills was so thorough and in general his observations were so exhaustive, considering the limited material, that it is worth while being cautious before suspecting him of an oversight, but I can not help thinking that what he took for palps was nothing but the foot. His figures (12, Figs. 1, 2) show it immediately behind the already shrunken velum and overlapped by the anterior gill-filaments. The two transverse lines may have been due to its being crumpled up, and the split towards the end of the ventral surface may have suggested two palps.

MONTREAL, Oct. 8, 1908.

SHORTER ARTICLES AND CORRESPONDENCE

SOME NOTES ON THE TRADITIONS OF THE NATIVES OF NORTHEASTERN SIBERIA ABOUT THE MAMMOTH

THE traditions of the Yukaghir very often mention the mammoth. They have a special name for him, xolhut. The spirit of the mammoth (xólhut-áibi—which means the mammoth's shadow), like the spirits of many other animals now living, appears in the rôle of a guardian spirit of certain shamans. A shaman assisted by the spirit or soul of a mammoth (*áibi* means shadow, spirit, and also soul) is regarded as the most powerful. According to this notion one might say that there was a time when the mammoth was a contemporary with man.

One Yukaghir tale relates to an episode in which the souls of two shamans (father and son) were riding on the back of a mammoth's shadow.

Another tradition tells of the disappearance of the mammoth. The creation of the mammoth was a blunder of the Superior Being. In creating such an enormous animal the Creator did not take into consideration the size of the earth and its resources. Our earth could not stand the weight of the mammoth and its vegetation was not sufficient to feed the mammoth race. The mammoth fed on tree trunks which he ground with his teeth, and in a short time the whole North of Siberia was deprived of trees. Hence is the origin of the northern tundra. In the beginning the earth had the form of an even plain, but by his weight the monster animal in moving about caused the formation of valleys and ravines in which rivers originated. In swampy or sandy places the mammoth sank into the ground and disappeared under the earth, where he froze during the winter. Often in the hole over him the water gathered into a lake. In this way the mammoth gradually disappeared from the earth's surface. This is why now whole cadavers of the animal are to be found in the frozen soil.

Among the Russianized Yukaghir of Nishnekolymsk I noted a tradition on the disappearance of the mammoth of a biblical

coloring. In the time of the flood Noah had to take besides the other animals a pair of mammoths. But when one of them put his fore legs on the raft he almost turned it over. Noah became terrified and quickly pushed his raft away from the monster. Thus all the mammoths perished.

Among the Chuckchee the mammoth is believed to be the reindeer of evil spirits. He lives underground and moves about through narrow passages. When a man sees a mammoth tusk protruding from the ground he must dig it up; otherwise the tusk will sink back into the ground. Once, it is said, some Chukchee found two mammoth's tusks protruding from the earth. They performed incantations and the mammoth came into sight. They lived on the mammoth for a whole winter.

A similar belief I found among the Tungus. On my way from the Okhotsk Sea to the Kolyma District over the Stanovoi Mountains I once spent a night on the banks of the lake "Kémemnan" or the "Mammoth's Lake." Concerning the origin of this name I was told that some time ago a family of wandering Tungus encamped beside the lake. When they arose in the morning they saw two pair of mammoth tusks appearing from under the ice. The Tungus fled on their reindeer horror-stricken, from the lake, but they all died except one small boy in their next encampment.

It is interesting to note that in the languages of the above-mentioned tribes the mammoth ivory is called "mammoth horn" (*e. g.*, the Yukaghir call it "xólhut-ónmun," *i. e.*, horn or antler of the mammoth), and not tusk or tooth, as if the people of to-day have no proper conception of the appearance of the mammoth. On the other hand, the natives know that the Siberian mammoth had a thick hairy tail and the "horns" grew from the mouth.

The export of mammoth-ivory from Siberia is still considerable. From the northern part of the Yakutsk Province alone (in greater part from the New Siberia Islands) the Moscow market receives 1800 pud (*i. e.*, 64,800 English pounds) every year. The weight of a pair of tusks is from 200 to 500 pounds, with an average of 360 pounds. Hence the yearly exportation of ivory of the Yakutsk Province is equal to the tusks of 152 mammoths. When we take into consideration the period of 200 years since the exportation began we find that tusks of 25,400 mammoths were sent out of the Yakutsk Province. It must be added that

MO. BOT. GARDEN

in former years the export was considerably greater than it is now.

WALDEMAR JOCHELSON.[1]

AGE OF TROTTING HORSE SIRES

THEORIES of heredity deduced from statistics always require critical examination. Statistics of heredity, like those of other subjects, offer striking possibilities to searchers for support of preconceived theories. I have recently completed some work with the trotting horse records, the result of which may be of interest inasmuch as it does not corroborate the results of other work in the same field.

Mr. C. L. Redfield has recently published a dynamic theory of development based largely on the statistics of the age of sires of average and of preeminent trotting horses. He assumes that by exercise a horse acquires "dynamic development," which facilitates speed and is transmitted. Dynamic development will naturally be greater in old than in young horses; in horses that are campaigned than in those not prepared for racing. Other things being equal, an old stallions' colts would inherit greater dynamic development and be faster than other colts sired by the same horse while younger. He found that the average trotting-bred horses, represented by the first one thousand animals listed in the Index Digest, were sired by stallions at an average age of 9.43 years. Representing the superior trotting horses by the 2.10 list, he based his calculations on the males appearing in four generations of each pedigree. The average time between generations in the male line in this instance was found to be 14 years; the sires were therefore practically 13 years old at the time of service. The difference between 9.43 and 13 years as the ages of sires of average and 2.10 horses is a very striking one and forms the basis of argument for the transmission of the dynamic development attributable to advanced age.

The matter of inheritance of dynamic development produced by racing, I propose to discuss at another time.

[1] Leader of the Riabouschinsky Expedition to Kamchatka, the Aleutian, Komandorski and Kurile Islands. Organized by the Imperial Russian Geographical Society. From 1900 connected with the Jesup North Pacific expeditions of the American Museum of Natural History. This contribution will be of very great interest both to ethnologists and zoologists.—H. F. O.

The following is from Mr. C. L. Redfield's recapitulation of his theory published in the *Horse World*, issue of February 27, 1906:

I said that I took one thousand registered stallions, alphabetically, from the *Index Digest* of the Register, and calculated the ages of their sires at the time when these registered stallions were foaled. From these I determined that the average time between generations in the male line was 10.43 years, which would give the average age of sires as 9.43 years at the time of service. I then said that, making all reasonable allowances for errors, the average time between generations in the male line might be set down as between 10 and 11 years, and that this period might be used as a standard in testing the age part of the theory. So far no one claims to have tested the accuracy of my calculation; no one claims that the figures I gave were wrong; and no one has said that these figures can not properly be used as a standard; yet if I am to be controverted, one of the first things to be done **is to dispute the accuracy of my standard.**

I then took the entire list of 2.10 trotters as an appropriate class of animals to be used in testing the inheritance of dynamic development, and I calculated the ages of their male progenitors for four generations. The number of animals involved was over five thousand and I gave the average time between generations in the male line for the production of 2.10 trotters as being approximately 14.00 years. This is an average of nearly 40 per cent. over the standard average determined from the Register, and my explanation of this remarkable difference was that it indicated the inheritance of acquired dynamic development. So far no one has disputed the accuracy of my computation and no one has attempted to give any other explanation of such an unusual divergence from the natural order of things.

Am I right or am I wrong? If I am wrong will some one please come forward with a better explanation.

It is to be noted that in the case of the average horses represented by the first thousand in the *Index Digest*, the ages of their *immediate* sires only were computed, and found to average 9.43 years; whereas in the case of the horses in the 2.10 list *all the sires appearing in the first four generations* were brought in. Assuming 14 years to be correct for the average time between generations, this carries us back 56 years.

The first horse that was uniformly successful as a sire of speed was Hambletonian 10 foaled in 1849. In the sixties this horse's reputation as a sire of speed was established and he did heavy stud service until the time of his death in 1873.

This was the real beginning of the trotting breed of horses. During the later years of the life of Hambletonian 10 and subsequent to his death his sons were patronized by owners of well-bred and speedy mares. The more successful of these sons naturally received heavy stud patronage as long as they remained serviceable. When the grandsons of Hambletonian 10, with two generations of speed-producing sires back of them and out of selected female ancestry, came into service, it was found that in many instances they sired faster colts than did their sires or grand sire. Only in more recent years were representatives of popular families used for stud purposes in earlier life.

In view of these facts, I deem it unfair to base a conclusion upon a comparison of two results, one of which (13 years as the average age at time of service of sires in four generations back of horses in the 2.10 list) comes largely from an investigation of the formative period of the breed, while the other (9.43 years as the average age at time of service of immediate sires of average horses) mainly refers to more recent conditions.

If the figures 9.43 and 13.00 had been derived by similar means their value would be unquestionable. A really fair comparison would demand the same procedure in one case as in the other. Either all sires in the four generations of the thousand horses should be used or else only the immediate sires of those in the 2.10 list.

Assuming 9.43 to be correct for the average age of the sires when they produced the first one thousand horses in the *Index Digest*, I have attempted to secure a similar figure for the immediate sires of the horses in the 2.10 trotting list as published in "Yearbook," Volume 22. The list published in that volume contains 279 horses. In thirty cases the records failed to show the horse's age. In seven cases the age of the sire is not given. This leaves 242 of the 279 in the list for which the ages are shown.

Below are given two extremes and the average for 242 horses regarding which there exists no uncertainty:

Horse	Foaled	Sire	Sire foaled	Age of Sire at Time of Service
Wentworth 2.04½	1903	Superior	1879	23.
Dolly Dillon 2.06½	1895	Sidney Dillon	1892	2.
Average for 242 horses				9.41

Of the 242 horses,
1 was sired by 2 year old stallion
11 were sired by 3 year old stallions
17 were sired by 4 year old stallions
30 were sired by 5 year old stallions
19 were sired by 6 year old stallions
21 were sired by 7 year old stallions
21 were sired by 8 year old stallions
25 were sired by 9 year old stallions
14 were sired by 10 year old stallions
17 were sired by 11 year old stallions
8 were sired by 12 year old stallions
13 were sired by 13 year old stallions
8 were sired by 14 year old stallions
9 were sired by 15 year old stallions
6 were sired by 16 year old stallions
6 were sired by 17 year old stallions
1 was sired by 18 year old stallion
4 were sired by 19 year old stallions
3 were sired by 20 year old stallions
0 were sired by 21 year old stallions
6 were sired by 22 year old stallions
2 were sired by 23 year old stallions

Taking 9.43 years as the average age of sires of average horses and substituting 14 by 9.41 years as the average age of sires of 2.10 trotting horses, it is evident that the records do not reveal any superiority of the old sire over the younger one.

F. R. MARSHALL.

OHIO STATE UNIVERSITY.

THE OCCURRENCE OF BATRACHOCEPS ATTENUATUS AND AUTODAX LUGUBRIS IN SOUTHERN CALIFORNIA

RECENTLY the salamander *Autodax lugubris* has been found near Los Angeles, Cal.[1] So far as I know, until this animal was reported no salamanders were known to live in southern California out from the mountains, although in the mountains and cañons of the foothills here and there as far as San Diego, another characteristic Pacific-coast salamander, *Diemyctylus*

[1] Miller, L. H., AM. NAT., Vol. XL, pp. 741–742.

torosus, has long been known. I have found it commonly in a number of cañons of the San Gabriel range and heard of it in other parts of southern California; in some places it seems to be quite abundant.

Two years ago last spring, just after the winter rains were over, a salamander was brought into the laboratory. It had been found in a garden near an orange orchard in Claremont, Cal., about four miles from permanent flowing water of the mountains and several hundred feet above subterranean water; the only water that could come to it was from rains and from irrigation. It was a full-grown specimen of *Batrachoceps attenuatus*. Some weeks later in the early part of June another full-grown specimen was brought in from another locality near Claremont. This time it was from a large, dry, uncultivated area and was found under a stone. A few hundred feet from the place where it was found there was a deep well. I afterward learned that ten or more years earlier a pond of considerable extent had covered this place.

During the winter of 1906–7 two small salamanders were sent to me from San Diego. They were half-grown *B. attenuatus*. The identification of these four specimens extends the known range of this species some hundreds of miles.

In May of this year a number of other salamanders were obtained from well up in the mountains north of Claremont, a number of specimens of *B. attenuatus* and two full-grown specimens of *Autodax lugubris*. The specimens of Autodax were found in a narrow crevice in a high rocky wall. This sort of a location is quite different from the other places where Autodax has been found.

Judging from the character of the land and water of Lower California it seems quite probable that one or all of the species mentioned in this note may occur farther south than San Diego.

WILLIAM A. HILTON.

POMONA COLLEGE, CLAREMONT, CAL.

NOTES AND LITERATURE

EXPERIMENTAL EVOLUTION

The Effect of the Environment upon Animals.—The second volume of Bachmetjew's great work, "Experimentelle Entomologische Studien" (1), will be welcomed by all who are interested in the effect of external factors upon organisms. It will doubtless surprise many that, although dealing almost exclusively with insects, the author reviews more than 1,200 papers. Even so, seasonal dimorphism, protective coloration mimicry and parthenogenesis are only touched upon incidentally as it is intended to take them up in a later volume. Furthermore, practically none of the literature since 1905 is included. The first 600 pages of the book are taken up with short abstracts arranged in chronological order within appropriate groupings. These abstracts are then rearranged—often being repeated verbatim—in the "theoretical part" according to their bearing upon special problems. Although the author states his opinions concerning the significance of the data thus brought together, the reader is largely left to draw his own deductions, as it seems to have been the aim of the author to make a handbook to the literature of experimental entomology rather than a dissertation in support of his own views. There can be little room for doubt in view of this immense amount of evidence that environmental factors are responsible for many—perhaps most—of the variations and aberrations among insects. However, there is, as yet, little proof that they produce heritable modifications such as we believe real species to be made of. In this regard Tower's work with Leptinotarsa is a remarkable exception. Practically all the results so far obtained, while interesting and important, belong to physiology rather than to evolution.

Federly is continuing his work concerning the effect of external conditions upon the scales of Lepidoptera. A recent paper (2) reviews the literature of albinism and gives certain original observations. True albinism seems to be rare. However, cases of "pseudo-albinism," due to a reduction in the size of the scales but not in the intensity of the pigment nor in the number of

pigment-bearing scales, are fairly common. This condition probably arises through an inhibiting action of the environment upon the "scale mother cells."

An interesting case of an environmental effect which is not easily reversed is given by Marchal (3). *Lecanium corni*, a scale insect, becomes *L. robiniarum* when reared upon *Robinia pseudo-acacia* instead of its normal food plants, but the reverse experiment does not succeed.

Salamanders are a close second to insects as favorite material for the experimental study of the effects of the environment. Powers has contributed a valuable paper (4) on the causes of variation in *Amblystoma tigrinum* and promises proof that certain of these are inherited or at least perpetuated by reason of inheritance. Differences in the amount and character of the food produce remarkable modifications in the structure of the animal. If, as is hinted, variations in the appetite are inherited, we should have an interesting case of indirect transmission of characters. Among the conclusions the author says:

"Specific characters, in species which vary as *A. tigrinum* varies, are, after all, strongly determined by environing conditions. There is nothing new in this. But the study of this species seems to me to lend it new weight and confirmation. If the broad head and large teeth of the cannibal are acquired characters—and they conform to the definition of such—what are the narrow head and smaller teeth of the customary daphnid-feeder? Are these specific and congenital characters? They are more frequent, more "typical" in the species, but I am forced to conclude that they are so chiefly because daphnids are numerous and constitute a convenient and stimulating food. And the same may be said of nearly all specific characters; so readily are they modified by a changed environment that we must conclude they are, in reality, equally determined even by an unchanged environment. Congenital tendencies in such species are not definitely specific, but only indefinitely specific. In this species, indeed, they are not always even definitely generic."

Mr. Powers naturally points out that many of our catalogued "species" are merely ontogenetic and believes that "the zoologist must soon admit that the final test of many species must lie in the rearing, and that, too, under controlled conditions." We may, perhaps, go further and say that this is the test of all species, but that it is not worth while to apply the test in all cases. It is probably true that many of our so-called species are not orthodox species but are the results of reversible physiological

changes in the soma. However, they are the species as we have them and it seems a hopeless task to go through the animal kingdom and sort the named forms into "ontogenetic" species and "orthodox" species. We shall probably be forced to recognize that the names we give are merely convenient shorthand descriptions of certain organisms, some of which are extremely stable as to form and coloration, others not so much so. Our problem is, then, to find out as much as we can about the causes which bring about the differences which we note.

A new journal, *Zeitschrift für Induktive Abstammungs- und Vererbungslehre*, has just been started. With Baur, Correns and other authorities as editors, much is to be expected of it.

FRANK E. LUTZ.

LITERATURE

1. 1907. Bachmetjew, P. Experimentelle Entomologische Studien vom physikalisch-chemischen Standpunkt aus. Zweiter Band. Einfluss der äussern Faktoren auf Insekten. xcvi + 944 pp. with 25 plates. Sophia.
2. 1908. Federley, Harry. Uber den Albinismus bei den Lepidopteren. *Acta Societatis pro Fauna et Flora Fennica*, XXXI, No. 4.
3. 1908. Marchal, P. Comptes rendus Soc. de Biologie, July. LXV, No. 24.
4. 1907. Powers, J. H. Morphological Variation and its Causes in Amblystoma tigrinum. *Studies from the Zoological Laboratory, the University of Nebraska*, No. 71. 77 pages with 9 plates.

EXPERIMENTAL ZOOLOGY

The Influence of the Size of the Egg and Temperature on the Growth of the Frog.[1]—What determines the difference in size of two animals? It is the difference due to greater or less number of cells, or, perhaps, to a difference in the size of their cells? Does the animal grow by adding more new cells, or by increasing the old cells? These are some of the problems which confront the student of the phenomenon of growth in the animal and plant kingdom alike.

The paper, the subject of this review, contains an account of experiments which attempt to throw light upon these problems.

[1] Einfluss der Eigrösse und der Temperatur auf das Wachsthum und die Grösse des Frosches und dessen Zellen. Von Robert Chambers, *Arch. für Mikroskopische Anatomie und Entwicklungsgeschichte*, Vol. 72, Part 3. pp. 607–661, 1908.

Chambers experimented with eggs of *Rana temporaria* and *R. esculenta*, and his object was to determine how the initial size of the eggs and temperature affect the size of developing embryos. He found that the eggs of both species show considerable variations in size, that are in no way connected with the prevailing temperature of the locality from which those eggs are collected. The average size of eggs varies not only with the species or locality, but also with each individual frog. Furthermore, eggs laid by one frog also present variations in size, which, in one case, were 1.8 mm., 1.2 mm., 1.15 mm., and 1.05 mm. in diameter. The eggs measuring 1.15–1.20 mm. were most abundant.

Contrary to what one might expect, there is no relation between the size of frogs and the size of eggs which they lay, and small frogs with large eggs as well as large frogs with small eggs are frequently found.

In the first place Chambers undertook to determine the relation of the size of an egg to the rate of its development and subsequent growth of the embryo. He divided eggs of a single frog into lots according to their sizes, and found, on rearing those, that small eggs have a tendency to develop slightly faster than large eggs. This tendency is marked only in the early stages, for as the tadpoles commence to feed those developing from large eggs grow faster and pass through metamorphosis sooner.[2] On rearing eggs of two lots, one containing eggs of large and uniform size, the other containing eggs of various sizes, it was found that the size of tadpoles varied considerably in favor of the former. Besides, the tadpoles of the first lot have all metamorphosed in course of two weeks, while two months have elapsed before the tadpoles of the second lot had all metamorphosed. There is one point in connection with this experiment on which unfortunately Chambers gives no information, and yet it may alter the conclusion drawn from the experiment. He mentions that there were 70 eggs in the first lot and 100 eggs in the second lot. If the eggs of both lots were distributed in an equal number of dishes there must have been fewer eggs of the large size than of the mixed sizes to each dish. The difference in the rate of development and in the size of tadpoles might have been therefore caused by the more or less crowded condition of the eggs, and not by the large or small initial size of the eggs. In fact, Chambers resorts to this factor of the number of eggs de-

[2] See page 7.

veloping in a dish to account for the fact that in experiment with eggs of 1.81 mm. and 1.20 mm. in diameter, the eggs of both sizes developed equally fast. The less crowded condition, he thought, compensated in that case for the small size of the eggs. The question as to whether or not the initial size of the egg is a determining factor in the rate of development seems to me, therefore, still an open question.

Next, Chambers investigated the influence of the size of the eggs upon development at different temperatures. Eggs of *R. temporaria* of the same size were reared separately under temperatures ranging from 10° to 25° C. He found in this case of *R. temporaria*, which spawns early in the spring, that both large and small eggs develop at low temperatures, but only the large eggs are capable of resisting higher temperatures. On the contrary, in case of *R. esculenta*, which spawns in May and June, all eggs develop well at high temperature (19°–27° C.) and only the large eggs develop at low temperature (10°–12° C.). Chambers therefore concludes that large eggs are more efficient in withstanding extremes of temperature.

He found, furthermore, that when eggs of the same individual are reared, under equal conditions of temperature, eggs larger or slightly smaller than those of normal size (the size of the majority of eggs is considered the normal size) develop to advanced stages, but the extremely small eggs invariably die out while yet in the early stages of development. In a lot of eggs, where the normal size was 1.5 mm. only 8 out of 23 eggs measuring 1.15 mm. in diameter and none of those measuring 1.05 mm. reached an advanced stage. Chambers is strongly inclined to think that there is a set limit to the size of the egg of a given species, beyond which it can no longer vary without losing its power of development. But the failure of abnormally small eggs to develop can also be interpreted differently, since the exceptionally small size may be due to the circumstance that the eggs have not yet attained full maturity.

Chambers states that large tadpoles develop always from large eggs, and that the ratio between the volumes of different eggs is maintained more or less constant during the early stages of development, *i. e.*, the tadpoles are in the same relation to each other, as regards volume, as the eggs from which they have developed.

Regarding the cellular elements of the young developed from

large or small eggs, Chambers found from his study of sections of various organs and tissues (lens, ear-vesicle, rectum, epidermis, cartilage, muscle-fibers and blood-corpuscules), that the size of the cells of a tadpole or young frog is in direct relation to the size of the examined individual. This in general agrees with the results from my own work, which I hope to publish in the near future, on the cells of large and small salamanders.

Since, as was shown above, the size of the embryo depends upon the size of the egg from which it develops, Chambers draws the further conclusion that the size of cells of an animal is determined by the initial size of the egg from which it has developed.

In another experiment, where eggs of *R. temporaria* were reared at two temperatures of 10° and 25° C., the tadpoles of the first set (10° C.) metamorphosed two months later than those of the second set (25° C.), but the young frogs developed in the medium with a low temperature (10°) were fully one and one half times as large as those developed at a higher temperature. Whether this large size was due to the low temperature or to the fact that the tadpoles had been growing two months longer before metamorphosing, this point is not made clear. However, on examining cells from the epidermis and rectum Chambers found that the differences in total size of frogs, developed at a high or a low temperature, extend also to their cells, so that large specimens have correspondingly larger cells than small specimens.

But the initial size of the eggs and the temperature of the medium are not the only factors determining the size of the tadpoles and young frogs, because large and small individuals may develop even from eggs of uniform size and under similar conditions of temperature. What has been found in regard to the variations in size of the eggs may of course be also true in case of the sperms, which might thus be a factor determining the size of the young. At any rate, Chambers made an interesting observation that tadpoles developed from eggs of the same size begin to vary only after the supply of yolk has been exhausted and they have commenced to take in food. It is not improbable, therefore, that the variations in size result either from an insufficient amount of food available for some tadpoles, as is the case, for instance, in growing starfishes,[3] or else the tadpoles may consume unequal amounts of food under different conditions of health.

[3] Mead, A. D. On the Correlation between Growth and Food-supply in Starfish. AMER. NAT., Vol. 34, No. 397, pp. 17–23, 1900.

It is a matter of some interest that Chambers maintains that the cells of large and small individuals developed from eggs of uniform diameter are not of different but of the same size. Thus he leads us to believe, and in fact he states it explicitly at the close of his paper, that the principal factor determining the size of cells of an animal is the initial size of the egg from which it developed.

Without giving mention to some objections to this general conclusion, which might be made on the basis of Chambers' own experiments, I wish to point out that the figures of cells given in the text do not carry conviction, and, so far as I was able to make out, they do not bear out Chambers' contention. In the drawings of cells of blood-corpuscles, epidermis and rectum, which Chambers thinks to be of equal size, I find on careful examination that the cells are different. Of course, actual measurements of the cells could make this matter clear, but, unfortunately, there are no measurements given in the paper.

The introduction to the paper contains a résumé of a few works in one way or another related to the problem. This résumé of facts so widely scattered throughout the literature will doubtless be found useful.

The third part of the paper is devoted chiefly to extensive theoretical considerations and does not therefore come within the scope of the present review.

In conclusion I should like to call attention to some defects of a technical character, which obscure the meaning of the text and frequently confuse the reader. In the explanation to Fig. 1 it is said, for instance, that I marks a culture developed from eggs of similar size, and II marks those developed from eggs of different and not ascertained sizes. But in the text referring to this Fig. 1 it is said that "Kulture II wurde mit Eiern angefangen, welche von gleicher, ausgesuchten Grösse waren." Which of these data, whether those found in the text or in the explanation to the figure, are the correct ones the reader is at loss to know, while the understanding of this point is important. On p. 635 we find reference to Fig. "A" and Aa in text Fig. 2. As a matter of fact this reference was found to apply to Fig. a and a^a in the Text-fig. 5. In Table V in the third column the date of spawning is given as June 5, and the date of the first examination of the developing embryos is June 3.

There is, however, a more vital contradiction in the text. On p. 620 in a discussion of the facts presented in Table I we read: "Die kleineren Eier zeigten eine geringe Neigung sich schneller zu entwickeln." On p. 647 referring again to the Table I we read: "In den Furchungs- und Gastrula-Stadien zeigen die kleinen Eier die Tendenz, sich wenigerschnell zu entwickeln, als die grösseren Eier." And further on, p. 647, and referring again to the Table I, we read: " Da wir nun aber gesehen haben, dass die grossen und kleinen Eier sich gleichgut und gleichrash entwickeln (s. Tabelle 1) etc."

Thus it appears that the small eggs develop somewhat faster, and slower than the large eggs, and just as well as the large eggs!

SERGIUS MORGULIS.

PARASITOLOGY

Cestodes of Birds.—Fuhrmann has recently published (*Zool. Jahrb.*, Suppl. 10, Heft 1) a most valuable monograph on the Cestodes of Birds. He had at his disposal all the material from the great European museums and from the private collections of prominent European helminthologists, so that the work is vastly more valuable than a mere literary revision with studies on limited personal collections. In 1782 Gœze described 14 species of Tænia from birds; in 1819 Rudolphi listed 54 certain and 30 uncertain species, and in 1850 Diesing recorded 81 certain and 28 questionable species. Von Linstow's Compendium der Helminthologie and Nachtrag in 1889 gave references to 230 bird cestodes from 340 host species. In this investigation Fuhrmann had material from 200 more species of birds at his disposal and recorded in all some 500 cestode parasites from them. When one considers that 12,000 species of birds are known and Cestodes have been collected from 540 only, it is clear that many more new forms are to be expected; these are to come most prominently from extra-European lands. North America which Fuhrmann notes as relatively unexplored, will contribute its share and I may add that investigations in this field are already in finished manuscript as studies from my own laboratory.

Some of the general conclusions which Fuhrmann has reached as a result of his 12 years of work in this field are of wide interest. The distribution of cestodes among the various group of birds shows that a given species occurs only in a given group

of birds and hence is typical of it. Birds with similar food habits shelter often radically different cestode parasites both in species and in genera. On the other hand, related birds of different food habits often show similar genera among their cestode guests even though the species differ. A zoogeographic survey of the cestodes in the various groups of birds shows a sharp contrast between the species found in different regions and furnishes strong evidence of the value of parasites as aids in zoogeographic investigations. In this respect the cestodes are unquestionably of the greatest value in the light of Fuhrmann's studies.

It would be impossible to abstract the systematic portion of Fuhrmann's paper. Many of the doubtful and insufficiently described species of other authors are here positively evaluated after comparison of the original material. Each genus is characterized on the basis of the author's investigations and the type species designated. The other species are also listed with references to the appropriate literature and to all known hosts. The faunistic section contains a complete list of the hosts with their cestode parasites and a record of the geographic distribution. A good alphabetic index of families, genera, species and synonyms, together with a full bibliography, closes the paper. Though not stated specifically, the monograph appears to be confined to the Cyclophyllidea and all will await with great interest the publication by this author of further studies dealing with other groups of avian cestodes.

A paper by Plehn (*Zool. Anz.*, 33: 427) on a blood-inhabiting cestode designated Sanguinicola, is of especial interest both from the morphological and from the biological standpoint. The animal occurs in the blood system of Cyprinid fishes, being most frequently found in the bulbus arteriosus, and was originally described in 1905 as an aberrant rhabdocœl. In structure it agrees well with the few monozoic cestodes classed together as Cestodaria and often separated from other cestodes. The species does not reach full development in this host, or at least in the blood vessels, since no specimens with fully developed female organs have yet been found. The author conjectures that it is withdrawn by some blood-sucking parasite and undergoes further development in that host. In view of the size of the worm and its evident inability to reach even the superficial arterioles, such a life cycle seems at least unlikely. The confessedly imperfect account of the structure of this worm makes any dis-

cussion of its precise genetic relationships unwise and the proposed phylogeny of parasitic flatworms based upon it has therefore only a purely suggestive value.

The Harben lectures for 1908, which were delivered by Professor George H. F. Nuttall, of Cambridge, England, have been printed (*Jour. Roy. Inst. Pub. Health,* July–September, 1908). The topics covered are the ticks and the diseases which they transmit to man and domestic animals; the diseases are among the most important of those caused by animal parasites especially and are due to spirochætes, piroplasma and filaria. Nuttall's account, which is the most complete résumé available in this field, is notably lucid and scholarly in presentation.

HENRY B. WARD.

The Astrophysical Journal

An International Review of Spectroscopy and Astronomical Physics

Edited by George E. Hale and Edwin B. Frost, with the collaboration of J. S. Ames, A. Bélopol'sky, W. W. Campbell, Henry Crew, N. C. Dunér, C. Fabry, C. S. Hastings, William Huggins, H. Kayser, A. A. Michelson, Ernest F. Nichols, A. Pérot, E. C. Pickering A. Riccò, C. Runge, Arthur Schuster, and F. L. O. Wadsworth.

The Astrophysical Journal, an international review of spectroscopy and astronomical physics, is the only publication in the world devoted to this department of astronomy, in which so great progress has been made in recent years, and to which the name "the new astronomy" is often applied. It publishes in English original contributions from investigators in all parts of the world, together with translations of important papers communicated to foreign learned societies which would be inaccessible to most of its readers. Special attention is given to having its illustrations represent the highest quality of engraving available, and in this respect it is unexcelled among scientific publications. The Journal is the medium of publication of the astrophysical researches made at Yerkes Observatory, and at the newly established Solar Observatory of the Carnegie Institution; and all important astrophysical results obtained at the Lick Observatory are found in its pages. It contains a department of reviews, in which all books within its field receive critical notice.

Issued monthly except February and August. $4.00 a year; single copies 50 cents. Foreign postage 62 cents.

The Botanical Gazette

A Monthly Review of Botanical Science

Editors: John M. Coulter and Charles R. Barnes.

The Botanical Gazette is the leading American journal of botany, and its contents therefore represent the most recent advances in this science. The changes in the subject are now so rapid that the most recent textbooks must of necessity lag far behind. For this reason, the latest information in reference to important botanical subjects should be available to all students and teachers of botany. In addition to its original papers, which represent the best work in America, a special feature in the Botanical Gazette is its department of "Notes for Students," in which all the important botanical work in the world is reviewed each month; so that the journal gives a complete monthly record in brief of botanical progress.

Issued monthly. $7.00 a year; single copies 75 cents. Foreign postage 84 cents.

The Journal of Geology

A Semi-Quarterly Magazine of Geology and Related Sciences

Editors: T. C. Chamberlin, in General Charge, R. D. Salisbury, J. P. Iddings, Stuart Weller, R. A. F. Penrose, Jr., C. R. Van Hise, W. H. Holmes, S. W. Williston. Associate Editors: Sir Archibald Geikie, H. Rosenbusch, Charles Barrois, Albrecht Penck, Hans Reusch, Gerard De Geer, C. K. Gilbert, H. S. Williams, C. D. Walcott, J. C. Branner, W. B. Clark, O. A. Derby, T. W. E. David.

While cultivating all geological fields, the Journal of Geology is recognized as the foremost medium in English for the presentation of advanced views on the basal and philosophic phases of geology and related sciences. It is the special organ of the new cosmogony and of the fundamental revisions of current doctrine that grow out of it. The Journal also makes a specialty of advanced and critical methods of geological investigation and interpretation. While American in some special sense, it is also cosmopolitan. It has recently published papers relating to the geology of Europe, Asia, Africa, South America, Iceland, New Zealand, and the Falkland Islands. As a pronounced evolution of new views is in progress and is likely to grow in importance, the Journal will become more and more indispensable to every progressive geologist.

$3.00 a year; single copies 50 cents. Foreign postage 53 cents.

Address Dept. 62

THE UNIVERSITY OF CHICAGO PRESS

CHICAGO NEW YORK **William Wesley & Son, London**

The American Naturalist

A Monthly Journal, established in 1867, Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Organic Evolution and Heredity

CONTENTS OF THE MAY NUMBER

Geographical Distribution; Origin of the Bermuda Decapod Fauna. Professor A. E. VERRILL.
On the Interpretation of Certain Tropisms of Insecta. CHARLES THOMAS BRUES.
The Evolution of Tertiary Mammals and the Importance of their Migrations. Professor CHARLES DEPÉRET.
On Xerophytic Adaptations of Leaf Structure in Yuccas, Agaves and Nolinas. Professor J. F. MCCLENDON.
The Biological Laboratory of the Bureau of Fisheries at Wood's Hole, Mass.: Report of Work for the Season of 1907. Dr. FRANCIS B. SUMNER.
Heredity of Hair Form in Man. GERTRUDE C. DAVENPORT and CHARLES B. DAVENPORT.
Notes and Literature: *Echinodermata*—Renewed Interest in Recent Crinoids, H. L. C. *Animal Behavior*—Recent Work on the Behavior of the Higher Animals. Professor HERBERT S. JENNINGS.

CONTENTS OF THE JUNE NUMBER

The Ancestry of the Caudate Amphibia. Dr. ROY L. MOODIE.
The Spirochætes and their Relationship to other Organisms. Professor HENRY B. WARD.
The Faunal Affinities of the Prairie Region of Central North America. Dr. ALEXANDER G. RUTHVEN.
Physiology. Professor FREDERIC S. LEE.
Notes and Literature: *Biometrics*—Recent Contributions to Theory, Professor RAYMOND PEARL. *Protozoa*—Some Amœba Studies, G. N. C. *Experimental Zoology*—Regeneration, M.

CONTENTS OF THE JULY NUMBER

A New Mendelian Ratio and Several Types of Lethals. Dr. GEORGE HARRISON SHULL.
The Leg Tendons of Insects. Professor C. W. WOODWORTH.
Abnormal Incisors of Marmota Monax L. CHARLES A. SHULL.
A Note on the Coloration of Plethodon Cinereus. HUGH DANIEL REED.
Some Experiments on the Order of Succession of the Somites in the Chick. Professor MARIAN E. HUBBARD.
Dwarf Faunas. Professor HERVEY W. SHIMER.
Notes and Literature: *Ichthyology*—Life History of the Eel, Professor CHARLES A. KOFOID; The Valves in the Heart of Fishes, President DAVID STARR JORDAN. *Parasitology*—The Heredity Transmission of Germ Diseases; A Society for the Destruction of Vermin, H. B. W. *Plant Cytology*—Polar Organization of Plant Cells, Dr. BRADLEY M. DAVIS.

CONTENTS OF THE AUGUST NUMBER

The Mid-summer Bird Life of Illinois: A Statistical Study. Professor S. A. FORBES.
The Life Cycle of Paramecium when subjected to a Varied Environment. Dr. LORANDE LOSS WOODRUFF.
Placobdella Pediculata n. sp. ERNEST E. HEMINWAY.
Marine Laboratories and our Atlantic Coast. Dr. ALFRED G. MAYER.
Biometry as a Method in Taxonomy. Professor CHARLES LINCOLN EDWARDS.
Shorter Articles and Correspondence: The Genus Ptilocrinus, AUSTIN HOBART CLARK. A New Rhinoceros from the Lower Miocene of Nebraska, HAROLD JAMES COOK.
Notes and Literature: *Plant Cytology*—Some Recent Research on the Cilia-forming Organ of Plant Cells, Dr. BRADLEY M. DAVIS. *Ornithology*—Riddle on the Genesis of Fault-bars and the Cause of Alternation of Light and Dark Bars in Feathers, J. A. A. *Herpetology*—Ruthven's Variations and Genetic Relationships of the Garter-snakes, J. A. A. *Lepidoptera*—Hybrid Lepidoptera, Professor T. D. A. COCKERELL.

CONTENTS OF SEPTEMBER NUMBER

Some results of the Florissant Expedition of 1908. Professor T. D. A. COCKERELL.
Embryology of Myosurus Minimus. Dr. LEROY D. SWINGLE.
Another Aspect of the Species Question. Dr. J. A. ALLEN.
The Origin of the Lateral Eyes of Vertebrates Professor G. H. PARKER.
Notes and Literature: *Heredity*—Spurious Allelomorphism, Results of Some Recent Investigations, W. J. SPILLMAN. *Human Anatomy*—Pryor on Sexual and Family Variation in Centers of Ossification, C. R. B. *Plant Cytology*—Cytological Studies on Saprolegnia and Vaucheria. Dr. BRADLEY M. DAVIS. *Holothurians*—Holothurioidea, Professor CHARLES L. EDWARDS. *Enteropneusta*—Recent Literature on the Enteropneusta, Professor W. E. RITTER. *Vertebrate Paleontology*—Case on Pelycosauria of North America; Barnum Brown on the Conrad Fissure and on the Ankylosauridæ, Professor S. W. WILLISTON. *Parasitology*—The Evolution of Parasitism; Trypanosomes, H. B. W.

CONTENTS OF THE OCTOBER NUMBER

The Manifestations of the Principles of Chemical Mechanics in the Living Plant. Dr. F. F. BLACKMAN.
The Desiccation of Rotifers. D. D. WHITNEY.
On the Habits and the Pose of the Sauropodous Dinosaurs, especially of Diplodocus. Dr. OLIVER P. HAY.
Shorter Articles and Correspondence: Juvenile Substitutes for Smoking Tobacco. Professor WILLIAM ALBERT SETCHELL.
Notes and Literature: *Heredity*—Recent Studies in Human Heredity, Dr. F. A. WOODS. *Ornithology*—Riddle on the Cause of the Production of Down and Down-like Structures in the Plumages of Birds, J. A. A. *Vertebrate Paleontology*—New Fossil Mammals from Egypt, T. D. A. C.

Single Number 35 Cents **Yearly Subscription, $4.00**

The NATURALIST will be sent to new subscribers for four months for One Dollar

THE SCIENCE PRESS

Garrison, N. Y. **Sub-Station 84: NEW YORK** **Lancaster, Pa.**

VOL. XLIII, NO. 506 FEBRUARY, 1909

THE AMERICAN NATURALIST

A MONTHLY JOURNAL
Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

CONTENTS

		Page
I.	Charles Darwin and the Mutation Theory. CHARLES F. COX.	65
II.	Juvenile Kelps and the Recapitulation Theory. II. Professor ROBERT F. GRIGGS.	92
III.	Notes and Literature: *Plant Phylogeny*—The Origin of the Archegoniates, Dr. BRADLEY M. DAVIS. *Holothurians*—Clark's The Apodous Holothurians, W. K. FISHER. *Lepidoptera*—The Blue Butterflies of the Genus Celastrina, Professor T. D. A. COCKERELL. *Vertebrate Paleontology*—The Lysorophidæ; Stegocephala; The Cotylosauria; The Oldest Known Reptile; The Age of the Gaskohle; Bison Occidentalis; Nectosaurus; Callibrachion, Dr. ROY L. MOODIE. *Parasitology*—The Sleeping Sickness Bureau, Professor HENRY B. WARD. *Exploration*—Camp-fires on Desert and Lava, Dr. ROY L. MOODIE	107

THE SCIENCE PRESS

LANCASTER, PA. GARRISON, N. Y.

NEW YORK: SUB-STATION 84

The American Naturalist

MSS. intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS

Lancaster, Pa. Garrison, N. Y.

NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

Important New Scientific Books

PUBLISHED BY THE MACMILLAN COMPNY

Botany

The Origin of a Land Flora. A Theory based upon the facts of Alternation. By F. O. BOWER, Sc.D., F.R.S. With numerous illustrations.

Cloth, gilt top, xi+727 pp., illus., index, 8vo, $5.50 net.

NOTE.—A profound study in the morphology of the lowest forms of plants, with special reference to the development of their reproductive systems. The author endeavors to show that the present land flora has originated from an aquatic ancestor, and traces the methods of specialization to the land habit, and the establishment of the forms of the higher plants. A book of the highest importance not only to botanists but to biologists in general.

NEW AND STANDARD HAND-BOOKS ON AGRICULTURE, ETC.

Elements of Agriculture, Southern and Western. By W. C. WELBORN, B.S., M.S., M.P.A.

Cloth, xvi+329 pp., illus., appendix, glossary, index, 12mo, $.75 net.

NOTE.—This is a thoroughly modern treatise on farming as practiced in the Gulf States, from the point of view of the scientific agriculturist. It is adapted to school use, but is of practical service to any farmer in that part of the country. The author is vice-director of the Texas Experiment Station.

Re-issues of the highly valued Hand-Books known as the Garden Craft and Rural Science Series, edited by L. H. BAILEY, of Cornell University. Editor of "Cyclopedia of American Horticulture," "Cyclopedia of American Agriculture," etc.

The Principles of Fruit Growing. By L. H. BAILEY.
Tenth Edition, $1.50 net, by mail $1.66.

Irrigation and Drainage. By F. H. KING.
Fifth Edition, $1.50 net, by mail $1.68.

Principles of Vegetable Gardening. By L. H. BAILEY.
Sixth Edition, $1.50 net, by mail $1.68.

Bush Fruits. By FRED W. CARD.
Fourth Edition, $1.50 net, by mail $1.66.

Fertilizers. By EDWARD B. VOORHEES.
Tenth Edition, $1.25 net, by mail $1.38

Farm Poultry. By GEO. C. WATSON.
Sixth Edition, $1.25 net, by mail $1.42

Published By **The Macmillan Company** 64-66 5th Ave., New York

THE
AMERICAN NATURALIST

VOL. XLIII *February, 1909* No. 506

CHARLES DARWIN AND THE MUTATION THEORY*

CHARLES F. COX

PROFESSOR HUGO DE VRIES, in his American lectures on "Species and Varieties, their Origin by Mutation," claims that his work is "in full accord with the principles laid down by Darwin,"[1] and boldly asserts that Darwin recognized both "mutation" and individual variation, or "fluctuation,"[2] as steps towards what Professor Cope aptly called "the origin of the fittest." I think many persons unfamiliar with Darwin's writings must have been much surprised on reading Professor De Vries's statement, for it has been a common belief in the scientific world for many years that the establishment of the mutation theory would be fatal to Darwinism, or would at least take from it its most original and essential features. The perpetuation of this impression has been due, very largely, to Mr. Wallace and certain of his followers who have steadfastly refused to admit the possibility of the evolution of species and varieties by any form of saltation and have insisted more uncompromisingly than did Mr. Darwin himself upon the exclusive efficiency of selection exercised upon small, recurring individual fluctuations. In fact, many of Mr. Wallace's views have out-Darwined Darwin and yet Darwin, somewhat unreasonably, has been held responsible for them.

* Presidential address at the annual meeting of the New York Academy of Sciences, December 21, 1908.

[1] Preface by the author, p. ix.

[2] Second edition, p. 7.

Accordingly Darwin has been charged with a radicalism which he never professed and champions of a *supposed* Darwinism have felt called upon to do battle against theories which he never distinctly repudiated or which he might even have accepted if he had known of them. Thus, Professor Poulton, in his recently published "Essays on Evolution," attacks with great severity, under the name of "Batesonians," believers in the validity of mutation as a factor in the process of evolution, although, as he admits, "mutation was of course well known to Darwin."[3] Now, I think we are justified in saying that if mutation was "*known*" to Darwin, it must have been, and still is, a veritable fact; and, if evolution is a universal law of nature it can not, in that case, exclude mutation. We, therefore, who believe in general evolution are compelled to decide for ourselves whether mutation has taken place and is now occurring; and we who are really Darwinians—that is to say, we who believe that Darwin set forth correctly the essential steps in the evolutionary process—are interested in knowing whether he actually recognized the fact of "discontinuous variation" or mutation, and, if so, how he fitted it into or reconciled it with his system.

The essential factors in organic evolution, from the Darwinian point of view, are: (1) Variation, (2) inheritance, (3) over-reproduction, (4) competition, (5) adaptation, (6) selection and survival. The general explanation of these factors is as follows:

1. All organisms vary continually and in every part of their structures—that is to say, no two individuals are exactly alike in any particular.

2. Nevertheless, characters anatomical, physiological and psychological are in general transmitted to descendants; in other words, progeny essentially resemble their parents.

3. More animals and plants are brought into the world than can possibly find means of subsistence.

[3] "Essays on Evolution," 1908, p. xviii.

4. There results competition for what subsistence there is, or, as it is otherwise called, a struggle for life.

5. Since out of all the variations that occur in the constitutions or characters of organisms some must happen to be in directions to give their possessors an advantage, or advantages, in procuring the means of existence, as compared with other individuals of the same class, some of the new-born animals and plants are best adapted to their surroundings or "conditions of life."

6. These best-adapted forms ("the fittest") will win in the struggle for life and are figuratively said to be selected; the unfit will in the end be exterminated. The result is the origination (evolution) of new classes of organisms out of the old ones and their substitution for the earlier classes or groups.

Not one of these factors was originally discovered by Darwin, but he first discerned their interrelations and bound them together by a consistent and convincing philosophy. He, for example, was not the earliest observer of progressive change in the organizations and external characters of animals and plants, but no one before him had had the insight to perceive that this changeability was the manifestation of a force great enough to burst the artificial limits placed about the groups called species and varieties and to enable them to transform themselves into other groups better adapted to the changing environment. Before Darwin's time every one, of course, had ocular demonstration of the fact that there were differences between individuals and that descendants were not in every respect like their ancestors. There was universal belief, however, that these variations never exceeded certain narrow boundaries built round species like inviolable walls. Curiously enough, Darwin, who first broke down these boundaries, took the same individual variations as the principal foundations of his selection theory. He assumed—for he admitted that it could not be proved for any particular case—that these small differences, which ordinarily fluctuate about a cer-

tain average for each species or variety, are at times accumulated to such a degree as to carry all the members of the group forward to a new center of oscillation so as to constitute in effect a new group. It was not at first his idea that a single individual, or a small number of individuals, might occasionally develop evolutionary force enough to over-leap suddenly the imaginary boundary and become the nucleus of a new colony beyond; that is the substance of the mutation theory; and, while I think it can be shown that Darwin more or less clearly recognized the possibility of the occasional origin of permanent races by this method of saltation, there can be no doubt that he entertained a strong bias in favor of the evolution of species generally by slow and minute steps.

As far as cultivated plants and domesticated animals were concerned Darwin was willing to grant the widest range of variation and the most abrupt changes, but as to animals and plants in a state of nature he was more sparing of his admissions that great and sudden departures from specific types might occur. This tenure of the two points of view was due to his belief that the domesticated animals and plants were more variable than feral forms because of the direct influence of man upon their surroundings and habits of life. Inasmuch as his theory of the origin of species through natural selection is founded on analogy between the deliberate operations of breeders in choosing the most desirable individuals of their flocks and gardens, and the inevitable sifting out of feral forms through their competition with one another in the struggle for existence, it is difficult to see why Mr. Darwin hesitated about carrying the comparison to its logical conclusion in the admission that what we now call mutations, but what he referred to as "spontaneous variations," "sports," "monstrosities," etc., stand upon substantially the same basis in nature as in cultivation. According to the present-day views of scientific students of animal and plant breeding, I understand, there is no

good evidence that cultivated plants and animals are more subject to wide and abrupt variations than are those living under natural conditions. On this point Professor De Vries remarks that "it is not proved, nor even probable, that cultivated plants are intrinsically more variable than their wild prototypes."[4] As to distinct mutations, we must remember that plants and animals preserved and nurtured by man are constantly under the eyes of many thousands of pecuniarily interested observers, while those in a state of nature are closely studied by but a handful of scientific investigators. We must also remember that it is only within a few years that a small fraction of these men of science have been led to look for cases of mutation, while all gardeners, farmers and breeders have had the inducement of financial profit to watch for marked variations among their stock and to preserve such variations if desirable. The naturalists specially interested in evolutionary questions are exceedingly few in number, but their field of research is immensely extended and varied. The number of those who have raised animals and plants for gain, however, has always been large, though the number of forms which they have been called upon to consider have been relatively few. The two fields have consequently had exceedingly different degrees of scrutiny. But since De Vries and others opened up the subject an astonishing number of clearly proven cases of mutation have been discovered in very various classes of organisms, just as numerous paleontological evidences of evolution have been brought to light as a consequence of Darwin's turning men's minds in that direction.

As I have already intimated, Mr. Darwin undoubtedly dealt with numerous cases of mutation among domesticated animals and plants, and they gave him little or no intellectual disquietude. In his work on "Animals and Plants Under Domestication" he gives a long catalogue of "spontaneous variations" or "sports," many of which

[4] "Species and Varieties, their Origin by Mutation," 2d ed., 1906, p. 66.

he freely acknowledges were the starting points of new and constant races; and there is good reason to believe that some of them occurred before the animals and plants which underwent the sudden changes had been actually brought under domestication or cultivation; in fact, that the mutations themselves suggested to men the directions in which their breeding operations should be conducted. For example, take the case of the tumbler pigeon: Mr. Darwin remarks concerning this that "no one would ever have thought of teaching or probably could have taught, the tumbler pigeon to tumble,"[5] but it seems to me obvious that no one would ever have thought of accumulating slight variations in the direction of tumbling. It is much more reasonable to suppose that the birds which were artificially selected as the progenitors of the present race of tumbler pigeons actually tumbled—that is to say, they were mutants. As to the origin of domestic races through modifications so abrupt as to have been thought by Darwin entirely independent of selection, he gave it as his judgment, as late as 1875, that

> It is certain that the Ancon and Mauchamp breeds of sheep, and almost certain that the Niata cattle, turnspit and pug-dogs, jumper and frizzled fowls, short-faced tumbler pigeons, hook-billed ducks, &c. suddenly appeared in nearly the same state as we now see them. So it has been with many cultivated plants.[6]

Now, considering, as I said a moment ago, that Mr. Darwin's theory of the origin of species by means of natural selection has for its main foundation-stones facts derived from observation of the effects of man's selection among domesticated animals and plants,—without which, indeed, he admitted that he had no actual proof of the operation of natural selection,—it is difficult to realize the state of mind which led Mr. Darwin to add to the sentence just quoted the following caution:

> The frequency of these cases is likely to lead to the false belief that natural species have often originated in the same abrupt manner. But

[5] "Origin of Species," 6th ed., 1882, p. 210.

[6] Ans. and Plnts. Under Dom., 2d ed., 1875, Vol. II. pp. 409–10.

we have no evidence of the appearance, or at least of the continued procreation under nature, of abrupt modifications of structure; and various general reasons could be assigned against such belief.

I am not aware that Mr. Darwin ever presented definite and convincing reasons for the sharp demarkation here attempted and, indeed, I can not see how the state of knowledge in his time could have justified it, for, as I have already stated, mutations had not been much looked for among feral plants and animals. In fact, by absolutely excluding from his theory the idea that mutation could occur under nature, Mr. Darwin, by the force of his great authority and influence, would have prevented a careful weighing of the pros and cons, if the human mind had at that time been prepared to weigh them. It is practically only since the Darwinian hypotheses have themselves been subjected to prolonged scrutiny, and since De Vries and a few others entered upon detailed experimental examination of this particular subject, within the last twenty years, that the matter can be said to have received anything like scientific treatment.

But, after all, Darwin was not *wholly* prejudiced against a belief in the occurrence of mutations in nature, for he several times expressed the opinion that the establishment of such a fact would in some ways be an advantage to the evolution theory. For instance, in a letter of August, 1860, to W. H. Harvey, he says:

> About sudden jumps: I have no objection to them—they would aid me in some cases. All I can say is that I went into the subject and found no evidence to make me believe in jumps; and a good deal pointing in the other direction.[7]

This of course refers to discontinuous variations in organisms under natural conditions, for he had certainly found evidence to make him believe in similar variations among domesticated animals and plants. I think Mr. Darwin never specified the directions in which a belief in mutation would be a help to him, but, from casual remarks made in various places, I fancy he had in mind

[7] "More Letters," Vol. I, p. 166. See also, "Life and Letters," 1886. Vol. II, p. 333.

the way in which it would ease him over that difficult subject, the imperfection of the geological record, and would reconcile him with the physicists and cosmogonists who were not disposed to allow him the lapse of past time he required for the evolution of species by the accumulation of successive minute or "insensible" individual variations. But I will not discuss these points now. What I wish to dwell upon at the moment is that Darwin recognized and accepted the fact of mutation among animals and plants under domestication, although it is worth while to repeat the statement that some of his cases probably happened in a state of nature, since they occurred at the very beginning of, and were the points of origination for, man's selective operations. As Mr. Darwin himself says: "Man can hardly select, or only with much difficulty, any deviation of structure excepting such as is externally visible,"[8] which means, as I take it, that nature usually presents some quite manifest variation before artificial selection begins, and this must have been the case at the time when man's first choices were made, particularly when half-civilized and unobserving men began the cultivation of our now domesticated animals and plants. It is necessary to remember, however, in this connection, that the mutation theory, as interpreted by De Vries, requires for its starting point only a variation which marks a distinct separation of a form from its parent group without connecting gradations, and not necessarily any great or extraordinary change of characters; for, as he says: "Species are derived from other species by means of sudden small changes which, in some instances, may be scarcely perceptible to the inexperienced eye."[9] None the less it remains true that man is apt to select only striking variations and hence Mr. Darwin, in treating of "sports," or what we should now call mutants, among cultivated plants and animals, usually speaks of them as wide departures from type, or, rather, he deals only with such as *are* large deviations.

[8] "Origin of Species," 6th ed., p. 28.
[9] "Plant Breeding," 1907, p. 9.

Even when treating of organisms in a state of nature, however, he admits that "there will be a constant tendency in natural selection to preserve the most divergent offspring of any one species."[10] Returning to the subject of artificial selection, Mr. Darwin says:

> No man would ever try to make a fan-tail till he saw a pigeon with a tail developed in some slight degree in an unusual manner, or a pouter till he saw a pigeon with a crop of somewhat unusual size; and the more abnormal or unusual any character was when it first appeared the more likely it would be to catch his attention.[11]

In another place he says:

> It is probable that some breeds, such as the semi-monstrous Niata cattle, and some peculiarities, such as being hornless, &c. have appeared suddenly owing to what we may call, in our ignorance, spontaneous variation; . . . During the process of methodical selection it has occasionally happened that deviations of structure more strongly pronounced than mere individual differences, yet by no means deserving to be called monstrosities have been taken advantage of.[12]

Now, in his work on Animals and Plants under Domestication Darwin has given a long list of these widely varying forms from each of which has descended a new race conforming to his own test of a species, namely its possession of "the power of remaining for a good long period constant . . . combined with an appreciable amount of difference."[13] One of the most striking of these cases is that of the "japanned" or "black-shouldered" peacocks which have occasionally appeared "suddenly in flocks of the common kind," which "propagate their kind quite truly," which, according to good authority, "form a distinct and natural species," and which tend "at all times and in many places to reappear."[14] Mr. Darwin rejects the idea that these birds are the result of hybridization and reversion and declares in favor

[10] "Origin of Species," 6th ed., 1882, p. 413.

[11] *Ibid.*, p. 28.

[12] "Animals and Plants under Domestication," 2d ed., 1875, Vol. I, p. 96. See also, Vol. II, pp. 189–90.

[13] "More Letters of Charles Darwin," 1903, Vol. I, p. 252.

[14] "Animals and Plants under Domestication," 2d ed., 1875, Vol. I, pp. 305–7.

of their being "a variation induced by some unknown cause," and says that "on this view the case is the most remarkable one ever recorded of the abrupt appearance of a new form which so closely resembles a true species that it has deceived one of the most experienced of living ornithologists." In all points this case agrees with the modern idea of a mutation, even in the respect that it comes from a family of birds not usually considered very variable.

Concerning fowls Mr. Darwin remarks that

> Fanciers, whilst admitting and even overrating the effects of crossing the various breeds, do not sufficiently regard the probability of the occasional birth, during the course of centuries, of birds with abnormal and hereditary peculiarities. Whenever, in the course of past centuries, a bird appeared with some slight abnormal structure, such as with a lark-like crest on its head, it would probably often have been preserved from that love of novelty which leads some persons in England to keep rumpless fowls and others in India to keep frizzled fowls. And after a time any such abnormal appearance would be carefully preserved from being esteemed a sign of the purity and excellence of the breed; for on this principle the Romans eighteen centuries ago valued the fifth toe and the white ear-lobe in their fowls.[15]

But Mr. Darwin's cases of what we must regard as saltations are not confined to the animal kingdom. We might easily cull from his list numerous more or less pertinent examples under the peach, plum, cherry, grape, gooseberry, currant, pear, apple, banana, camellia, cratægus, azalea, hibiscus, althæa, pelargonium, chrysanthemum, dianthus, rose and perhaps other plants. Concerning useful and ornamental trees he says: "All the recorded varieties, as far as I can find out, have been suddenly produced by one single act of variation,"[16] and as to roses, he remarks on their marked tendency to "sport" and to produce varieties "not only by grafting and budding, but often by seed," and quotes Mr. Rivers as saying that "whenever a new rose appears with any peculiar character, however produced, if it yielded seed" he "ex-

[15] "Animals and Plants Under Domestication," 2d ed., Vol. I, pp. 242–4.
[16] *Ibid.*, p. 384.

pects it to become the parent of a new family." In this connection Mr. Darwin called attention to the now well-known fact that the mutative tendency is an inheritable one by citing the case of the common double moss-rose, imported into England from Italy about the year 1735, which "probably arose from the Provence rose (*R. centifolia*) by bud-variation," the White Provence rose itself having apparently originated in the same way.[17] He also called attention to the significant fact that many abrupt variations were not to be attributed either to reversion or to the splitting-up of hybrids. Thus he declares:

> No one will maintain that the sudden appearance of a moss-rose on a Provence rose is a return to a former state, for mossiness of the calyx has been observed in no natural species; the same argument is applicable to variegated and laciniated leaves; nor can the appearance of nectarines on peach-trees be accounted for on the principle of reversion.[18]

Further on in the same work he says:

> Many cases of bud-variation . . . can not be attributed to reversion, but to so-called spontaneous variability, as is so common with cultivated plants raised from seed. As a single variety of the chrysanthemum has produced by buds six other varieties, and as one variety of the gooseberry has borne at the same time four distinct kinds of fruit, it is scarcely possible to believe that all these variations are due to reversion. We can hardly believe . . . that all the many peaches which have yielded nectarine-buds are of crossed parentage. Lastly, in such cases as that of the moss-rose, with its peculiar calyx, and of the rose which bears opposite leaves, in that of the Imantophyllum, &c., there is no known natural species or variety from which the characters in question could have been derived by a cross. We must attribute all such cases to the appearance of absolutely new characters in the buds. The varieties which have thus arisen can not be distinguished by any external character from seedlings. . . . It deserves notice that all the plants which have yielded bud-variations have likewise varied greatly by seed.[19]

Now, Darwin was here treating of saltations among cultivated plants, but it is instructive to read in this con-

[17] "Animals and Plants Under Domestication," 2d ed., Vol. I, pp. 405-6.

[18] *Ibid.*, Vol. II, p. 242.

[19] "Animals and Plants Under Domestication," 2d ed., Vol. I, pp. 439–40.

nection the following passage in which he prepares the ground for a belief in the possibility of similar abrupt and wide variations under natural conditions. He remarks:

> Domesticated animals and plants can hardly have been exposed to greater changes in their conditions of life than have many natural species during the incessant geological, geographical, and climatal changes to which the world has been subject; but domesticated productions will often have been exposed to more sudden changes and to less continuously uniform conditions. As man has domesticated so many animals and plants belonging to widely different classes, and as he certainly did not choose with prophetic instinct those species which would vary most, we may infer that all natural species, if exposed to analogous conditions, would, on an average, vary to the same degree.[20]

But now let us take a specific example of spontaneous variability which deeply impressed Mr. Darwin. It is a case which was brought to his attention in 1860 by Professor W. H. Harvey concerning *Begonia frigida*, as to which Mr. Darwin says:

> This plant properly produces male and female flowers on the same fascicle; and in the female flowers the perianth is superior; but a plant at Kew produced, besides the ordinary flowers, others which graduated towards a perfect hermaphrodite structure; and in these flowers the perianth was inferior. To show the importance of this modification under a classificatory point of view, I may quote what Professor Harvey says, namely, that had it "occurred in a state of nature, and had a botanist collected a plant with such flowers, he would not only have placed it in a distinct genus from *Begonia*, but would probably have considered it as the type of a new natural order." . . . The interest of the case is largely added to by Mr. C. W. Crocker's observation that seedlings from the *normal* flowers produced plants which bore, in about the same proportion as the parent-plant, hermaphrodite flowers having inferior perianths.[21]

This was written in the first edition of "Animals and Plants under Domestication" (1868) and was allowed to stand in the second and last edition (1875). In both editions, however, Mr. Darwin made the statement in an entirely different part of the work, that "the wonderfully anomalous flowers of *Begonia frigida*, formerly described, though they appear fit for fructification, are

[20] *Ibid.*, Vol. II, pp. 401–2. See also *ibid.*, Vol. II, p. 278.

[21] "Animals and Plants Under Domestication," 2d ed., Vol. I, p. 389.

sterile.''[22] The last point, however, does not invalidate the claim to this new type of Begonia as a mutant, since the facts which determine its position in this regard are, first, the sudden appearance of the form bearing three kinds of flowers and, second, the production by seed of descendants also bearing three kinds of flowers.

It is very evident that this case troubled Mr. Darwin, for he referred to it a number of times and did not relish Professor Harvey's assertion that "such a case is hostile to the theory of natural selection, according to which changes are not supposed to take place *per saltum*," and Harvey's further declaration that "a few such cases would overthrow it (natural selection) altogether."[23] Sir Joseph Hooker attempted to explain the matter so as to weaken Professor Harvey's argument against the doctrine of natural selection, but Darwin himself wrote Hooker, saying:

> As the "Origin" now stands Harvey is a good hit against my talking so much of the insensibly fine gradations; and certainly it has astonished me that I should be pelted with the fact that I had not allowed abrupt and great enough variations under nature. It would take a good deal more evidence to make me admit that forms have *often* changed by *saltum*.

About the same time, namely early in 1860, Darwin wrote to Lyell on this subject, saying:

> It seems to me rather strange; he (Harvey) assumes the permanence of monsters, whereas monsters are generally sterile and not often inheritable. But grant this case, it comes that I have been too cautious in not admitting great and sudden variations.[24]

There is an added point of interest about this discussion in the fact that it is the earliest record in print of the consideration of saltation or mutation by Mr. Darwin.

You have doubtless noticed Mr. Darwin's protest against the belief in the occurrence of important changes "*per saltum.*" He uses this expression with disapproval a number of times and yet his condemnation of

[22] *Ibid.*, 1st ed., Vol. II, p. 166. Also *ibid.*, 2d ed., Vol. II, p. 150.
[23] "Life and Letters," 1886, Vol. II, p. 274.
[24] *Ibid.*, p. 275. Also, "More Letters," 1903. Vol. I, p. 141.

the idea involved is not entirely unqualified, as is shown by the following significant statement:

> On the theory of natural selection we can clearly understand the full meaning of the old canon in natural history, "Natura non facit saltum." This canon, if we look to the present inhabitants alone of the world, is not strictly correct; but if we include all those of past times, whether known or unknown, it must on this theory be strictly true.[25]

This I understand to be in effect a protest against deducing proof of separate creations from the imperfection of the geological record, coupled with an admission that saltation or mutation does, at least occasionally, occur among existing living forms. I trust you perceive the importance of the concession that *natura non facit saltum* is not strictly correct as applied to *the present inhabitants of the world.*

Having noticed Mr. Darwin's repeated use of the words *per saltum,* I now wish to revert to his frequent use of the words *monster* and *monstrosity* and to call your attention to the fact that they are not always employed with exactly the same meanings. Sometimes by "monstrosity" he evidently intends to indicate a mere deformity of the nature of an accidental injury, or aborted or perverted development, but more generally he refers to a deviation from type wide enough, or discontinuous enough, to exclude it from the category of variations to which he supposed the operation of natural selection must be confined. Among domesticated animals and plants, however, the word monster as used by him often meant no more than the word "sport." In most cases when he used this term or one of its derivatives he took care to explain that monstrosities could not be qualitatively separated from other kinds of variations. Thus, in writing to R. Meldola, in 1873, he says:

> It is very difficult or impossible to define what is meant by a large variation. Such graduate into monstrosities or generally injurious variations. I do not myself believe that these are often or ever taken advantage of under nature.[26]

[25] "Origin of Species," 6th ed., p. 166. See also *ibid.*, pp. 156, 234, 414.
[26] "More Letters," 1903, Vol. I, p. 350.

In the "Origin of Species" he wrote:

> At long intervals of time, out of millions of individuals reared in the same country and fed on nearly the same food, deviations of structure so strongly pronounced as to deserve to be called monstrosities arise; but monstrosities cannot be separated by any distinct line from slighter variations.[27]

He frequently repeats this statement and it is quite clear that he intends to convey the idea that all variations are merely quantitative; at any rate he failed to adopt a nomenclature that would enable his readers to judge as to the degrees of difference he meant to indicate by such adjectives as "insensible," "minute," "slight," "large," "wide," "sudden" and "abrupt," as applied to variations. I am convinced, however, that he had in mind an idea that there were two different kinds of variations, namely, first, what he oftenest called "individual variations," by which he referred to the ordinary differences between the single organisms of the same group, or what mutationists now call "fluctuations," and, second, those radical and generally extensive deviations from type which constitute an actual break with the species, variety or race, and which are substantially what we of these later times have named "mutations." There are places in Darwin's works where the two kinds of variation just mentioned are spoken of as "indefinite" and "definite" and as results, respectively, of the *indirect* and the *direct* action of the conditions of life, and once only, I think, he uses the term "*fluctuating variability*" as synonymous with *indefinite* variability.[28] Now I do not assume to say that the recognition of these distinctions by Mr. Darwin proves that he clearly foresaw the present-day mutation theory with its foundation in the principle of unit characters, but I think it is true that he had at least a glimpse of the coming modifications

[27] "Origin of Species," 6th ed., p. 6, also p. 33. See also "Animals and Plants Under Domestication," 2d ed., Vol. I, pp. 312, 322. Also "More Letters," 1903, Vol. I, p. 318.

[28] "Animals and Plants Under Domestication," 2d ed., Vol. II, pp. 280, 281, 345.

to be required in his own theory to meet the then dawning truth. De Vries declares that his own field researches and testing of native plants are based "on the hypothesis of unit-characters as deduced from Darwin's Pangenesis," which conception, De Vries points out, "led to the expectation of two different kinds of variability, one slow and one sudden."[29]

But the main point I wish to dwell upon at present is that Darwin recognized, at least dimly, a kind of variability the results of which were essentially different from the "individual" or "indefinite" variations, which mistakenly seemed to him alone capable of being acted upon by selection. He was sorely puzzled by what he saw and realized in this direction, for he had spent more than twenty years of intense thought in elaborating his theory that new species were evolved from older ones by the gradual building up of new characters from extremely small differences, and he feared that the admission of saltation in any form meant the undermining of the foundations he had labored so hard to construct. He had once said:

> When we remember such cases as the formation of the more complex galls, and certain monstrosities, which cannot be accounted for by reversion, cohesion, &c., and sudden strongly-marked deviations of structure, such as the appearance of a moss-rose on a common rose, we must admit that the organization of the individual is capable through its own laws of growth, under certain conditions, of undergoing great modifications, independently of the gradual accumulation of slight inherited modifications.[30]

In the last edition of the "Origin of Species," however, which was published in the year of the author's death, although he introduces this apology: "In the earlier editions of this work I underrated, as it now seems probable, the frequency and importance of modifications due to spontaneous variability,"[31] he still later inter-

[29] "Species and Varieties, their Origin by Mutation," 2d ed., 1906, p. 689.

[30] "Origin of Species," 5th ed., 1869, p. 151.

[31] "Origin of Species," 6th ed., 1882, p. 171.

polates the following rather sweeping recantation:

> There are, however, some who still think that species have suddenly given birth, through quite unexplained means, to new and totally different forms; but, as I have attempted to show, weighty evidence can be opposed to the admission of great and abrupt modifications. Under a scientific point of view, and as leading to further investigation, but little advantage is gained by believing that new forms are suddenly developed in an inexplicable manner from old and widely different forms, over the old belief in the creation of species from the dust of the earth.[32]

In this sixth, and last, edition of the "Origin of Species" Mr. Darwin devotes to the task of answering criticisms made by St. George Mivart far more space than he had ever allowed to any other one critic and the passage just read is evidently one of those inspired by Mr. Mivart's attacks. The sore point with Mr. Darwin at that time was the doctrine of natural selection and, as I have already remarked, he had adopted the erroneous belief that this important principle must be greatly weakened if not entirely sacrificed if any form of saltation was to be admitted in nature. He had, therefore, wavered between his loyalty to his cherished hypothesis and his fearless devotion to truth. By this time, however, he had so long contemplated the possibility of the origin of new species and varieties through single long steps and had had so many convincing examples brought to his attention, that his hesitancy and doubt concerning the validity and sufficiency of the arguments urged in favor of this mode of evolution were ready to give way, and I regard the passage, which I am about to quote, as a virtual surrender on this point. The fact that, in this emphatic form, it was written at the close of his life, as his last word on this subject, and that he must have felt that it contained a concession very damaging to the theory to the establishment of which that life had been devoted, gives it, in my mind, a deeply pathetic significance. Mr. Darwin says:

[32] "Origin of Species," 6th ed., 1882, p. 424.

It appears that I formerly underrated the frequency and value of [variations which seem to us in our ignorance to arise spontaneously] as leading to permanent modifications of structure independently of natural selection. But as my conclusions have lately been much misrepresented, and it has been stated that I attribute the modification of species exclusively to natural selection, I may be permitted to remark that in the first edition of this work, and subsequently, I placed in a most conspicuous position—namely, at the close of the Introduction—the following words: "I am convinced that natural selection has been the main but not the exclusive means of modification." This has been of no avail. Great is the power of steady misrepresentation; but the history of science shows that this power does not long endure.[33]

The sting of this vehement declaration is in the underlying implication that the limitation placed upon the applicability of natural selection was deemed necessary because of Mr. Darwin's inability to free his mind from the belief that it could not act upon large and sudden variations as well as upon small and unimportant ones. This point of view seems illogical when we consider his repeated declaration that no qualitative distinction could be established between the two kinds of variation, but it may be partially accounted for by the fact that a slight confusion at times existed in his mind concerning the general *modus operandi* of natural selection, through which he attributed to it a *causal* power as well as a mere sifting effect. Both Lyell and Wallace took him to task for this double use of the term and, therefore, in the third edition of "the Origin" he attempted to clear up this point by means of this statement:

> Several writers have misapprehended or objected to the term natural selection. Some have even imagined that natural selection even *induces* variability, whereas it implies only the preservation of such variations as arise and are beneficial to the being under its conditions of life.[34]

Nevertheless, almost side by side with this explanation we find in the last edition of "the Origin," the following sentences which were allowed to come down from the first edition: "Natural Selection will *modify* the

[33] "Origin of Species," 6th ed., p. 421. See also, "Life and Letters," 1886, Vol. III, p. 243, and "More Letters," 1907, Vol. I, p. 389.

[34] "Origin of Species," 3d ed., 1861, p. 84.

structure of the young in relation to the parent, and of the parent in relation to the young.'"[35] "Natural Selection . . . will *destroy* any individual departing from the proper type.'"[36] If Darwin had adopted the simile of a sieve, so effectively used by De Vries, he would have drawn nearer to the recognition of the fact of "selection *between* species," even if he had not been prepared to assent to De Vries's counter proposition that there is no "selection *within* the species." He might also have escaped some of his apprehensions concerning the fate of adaptation, which he thought to be endangered by a belief in saltation; for the fact is that adaptedness is only another name for fitness, and this is a quality inherent in the organism and precedent to selection—that is to say, natural selection merely sifts out for preservation the *adapted* or fit, allowing the unadapted or unfit to perish. Now, it is impossible to see why forms both adapted and unadapted to their environment may not arise through mutation and thus be offered to the operation of selection. In fact, Mr. Darwin has supplied us with a good illustration of such a case in a rather naïve passage which has run through every edition of "the Origin," to the following effect:

> One of the most remarkable features in our domesticated races is that we see in them adaptation, not indeed to the animal's or plant's own good, but to man's use or fancy. Some variations useful to him have probably arisen suddenly, or by one step; many botanists, for instance, believe that the fuller's teasel, with its hooks, which can not be rivaled by any mechanical contrivance, is only a variety of the wild Dipsacus: and this amount of change may have suddenly arisen in a seedling.[37]

Surely, if Mr. Darwin could have looked at this case with a perfectly free mind, he must have perceived that the teasel's adaptation to man's needs would not have fallen if man had failed to exercise his power of selection; and that the adaptation was not weakened by the fact that it arose by a mutation. But that he was uncon-

[35] *Ibid.*, 6th ed., 1882, p. 67.
[36] *Ibid.*, 6th ed., 1882, p. 81.
[37] "Origin of Species," 6th ed., p. 22.

sciously biased in this matter is shown by an extract from a letter written to Asa Gray, in 1860, in which he says:

> I reflected much on the chance of favorable monstrosities (*i. e.*, great and sudden variation) arising. I have, of course, no objection to this, indeed it would be a great aid, but I did not allude to the subject [*i. e.*, in "the Origin"] for, after much labor, I could find nothing which satisfied me of the probability of such occurrences. There seems to me in almost every case too much, too complex, and too beautiful adaptation, in every structure, to believe in its sudden production.[38]

The idea involved in this passage is that adaptation is *produced*—rather than *preserved*—by natural selection and that, as natural selection must, according to Mr. Darwin's curious prepossession, act only upon slow and small changes of character, adaptation itself must necessarily be in every case a matter of gradual growth. This sort of argument appears to justify the fear shared by both Lyell and Hooker that Darwin was at times disposed to stake his whole case on the maintenance of an unnecessary assumption. Hooker wrote him as early as 1859 or 1860 that he was making a hobby of natural selection and overriding it, since he undertook to make it account for too much.[39] Darwin mildly protested that he did not see how he could do more than he had done to disclaim any intention of accounting for everything by natural selection.[40] In this discussion, however, it is apparent that while Darwin was overloading the theory of natural selection with a responsibility for the origin of the adapted or fit, he was at the same time unduly limiting it to only one class of the fit, namely those which had arisen by slow degrees. If he had taken the position that natural selection could and would operate upon any kind or any degree of variability, he need not to have imagined that his main doctrine was in jeopardy.

But though Mr. Darwin could be stirred by attack to a vigorous defense, and sometimes even to an *over*-defense, of natural selection, he contended, at other times, with equal vigor, that his main interest was with varia-

[38] "Life and Letters," 1887, Vol. II, p. 333.
[39] "More Letters," 1903, Vol. I, p. 135.
[40] *Ibid.*, Vol. I, pp. 172, 213.

tion, however produced, which was the necessary basis of the whole evolutionary process. He admitted, however, that the cause of variation was to him inexplicable and, like all beginnings, it remains to this day a deep mystery. Darwin said of it:

> Our ignorance of the laws of variation is profound. Not in one case out of a hundred can we pretend to assign any reason why this or that part has varied.[41]

In another place he remarks:

> When we reflect on the millions of buds which many trees have produced before some one bud has varied, we are lost in wonder as to what the precise cause of each variation can be.[42]

He never definitely undertook to solve this mystery, though he reflected and reasoned on it much. The nearest he came to formulating a law concerning it was the expression of his conviction that variability was more a matter of organic constitution than a result of external agencies. Thus he declares:

> If we look to such cases as that of a peach tree which, after having been cultivated by tens of thousands during many years in many countries, and after having annually produced millions of buds, all of which have apparently been exposed to precisely the same conditions, yet at last suddenly produces a single bud with its whole character greatly transformed, we are driven to the conclusion that the transformation stands in no *direct* relation to the conditions of life.[43]

From examples like this Mr. Darwin deduced a "general rule that conspicuous variations occur rarely, and in one individual alone out of millions, though all may have been exposed, as far as we can judge, to nearly the same conditions"[44] and while this is, in a general way, in accordance with the admission of De Vries that although mutations are "not so very rare in nature,"[45] the numbers "under observation are as yet very rare,"[46] we shall see a little later that Mr. Darwin's deduction is not

[41] "Origin of Species," 6th ed., p. 131.
[42] "Animals and Plants Under Domestication," 2d ed., Vol. II, p. 281.
[43] *Ibid.*, 2d ed., Vol. I, p. 441. See also, *ibid.*, Vol. II, pp. 277, 279, 282.
[44] "Animals and Plants Under Domestication," 2d ed., Vol. II, p. 276.
[45] "Species and Varieties, their Origin by Mutation," 2d ed., p. 597.
[46] *Ibid.*, p. 8.

strictly accurate since it excludes the idea of a whole genus or species or variety mutating at once.

While on this subject, I may mention that Mr. Darwin anticipated the doctrine of the mutationists to the effect that "when the organization has once begun to vary, it generally continues varying for many generations."[47] But as to variability having periods of activity Mr. Darwin's opinion seems to have been unsettled. In a letter to Weismann, in 1872, he remarks on the strangeness "about the periods or endurance of variability,"[48] but in a letter to Moritz Wagner, in 1876, he says:

> Several considerations make me doubt whether species are much more variable at one period than at another except through the agency of changed conditions. I wish, however, that I could believe in this doctrine, as it removes many difficulties.[49]

Practically this is the dilemma of the mutationists of the present day: they are not in a position to prove that plants and animals have periods of mutation, but they assume that it must be so, because the belief "removes many difficulties."

One of Darwin's perplexities, however, has been explained away, as I have already pointed out, by the discovery that mutation is not confined to a single case out of millions of individual forms, nor even to a single generation out of a long genetic line, but that, as in the case of the Œnotheras (evening primroses), a whole genus is likely to be in a mutating condition at the same time, producing from each of several species numberless individual mutants, which are themselves often in a mutating condition, the parent stock meanwhile remaining perfectly constant. Such has been the case with *Œnothera* (*Onagra*) *lamarckiana*, which, while throwing off, since it has been under scientific observation, in large numbers not less than a dozen elementary species and retrograde varieties, has bred true to its original type through at least one hundred and sixteen years, although there is

[47] "Origin of Species," 6th ed., p. 5.
[48] "Life and Letters," 1886, Vol. III, p. 155.
[49] *Ibid.*, p. 158.

considerable proof that it is itself a mutant from *Œnothera grandiflora*, and none whatever for the assertion, often made, that it is a hybrid. As at least nine of its mutants have also bred true through many generations in pedigree cultures and doubtless had been constant forms for a long time in a state of nature, there appears to be no ground for Darwin's fear that, granting the occurrence of mutation, the mutants would be liable to speedy extermination through inability to propagate. Of course this would not be the case with even a single self-fertilizing plant and it would not be true with animal mutants if, like plant mutants, they were produced in numbers by the mutating stock. As to swamping by intercrossing, it has been shown that, under Mendel's law, in the extreme case of the production of a solitary mutant obliged to cross with the parent form, if it possesses characteristics having a certain relation to the parent, it can establish a race like itself and even supplant the parent form, if it is only *as well* fitted for the battle of life as is the progenitor.[50]

If Darwin had known these facts he would not have written, or he would have greatly amended, the following passage:

> He who believes that some ancient form was transformed suddenly through an internal force or tendency into, for instance, one furnished with wings, will be almost compelled to assume, in opposition to all analogy, that many individuals varied simultaneously. It can not be denied that such abrupt and great changes of structure are widely different from those which most species apparently have undergone. He will further be compelled to believe that many structures beautifully adapted to all the other parts of the same creature and to the surrounding conditions, have been suddenly produced; and of such complex and wonderful co-adaptations, he will not be able to assign a shadow of an explanation. He will be forced to admit that these great and sudden transformations have left no trace of their action on the embryo. To admit all this is, as it seems to me, to enter into the realms of miracle, and to leave those of science.[51]

Of course Mr. Darwin was not entirely oblivious to the fact that every important advance in knowledge must

[50] See Lock's "Variation, Heredity and Evolution," 1906. p. 205.

[51] "Origin of Species," 6th ed., p. 204. See also, *ibid.*, p. 202.

have the appearance, at first, of a move into a region of mystery and uncertainty. The lapse of time and the growth of familiarity with it are necessary to the reclamation of a *terra incognita.*

Before leaving this branch of my subject, I desire to call your attention to the very interesting fact that Mr. Darwin himself once conducted a long series of experiments which, it can hardly be doubted, resulted in the production of mutants and that he just missed the discovery of principles which are now the basis of scientific pedigree cultures and are occupying the attention of investigators of the problems of variation and heredity. In a letter to J. H. Gilbert, dated February 16, 1876, Mr. Darwin writes:

> Now, for the last ten years I have been experimenting in crossing and self-fertilizing plants; and one indirect result has surprised me much, namely, that by taking pains to cultivate plants in pots under glass during several successive generations, under nearly similar conditions, and by self-fertilizing them in each generation, the colour of the flowers often changes, and, what is very remarkable, they became in some of the most variable species, such as Mimulus, Carnation, &c., quite constant, like those of a wild species. This fact and several others have led me to the suspicion that the cause of variation must be in different substances absorbed from the soil by these plants when their powers of absorption are not interfered with by other plants with which they grow mingled in a state of nature.[52]

The point I particularly wish you to notice in this case is that Mr. Darwin was employing practically the methods now used by Professor De Vries, Professor MacDougal and others who are engaged in species testing, by growing naturally variable or mutating plants under conditions of rigid control, so as to exclude crossing or, as De Vries calls it, *vicinism.* In this view of the matter, it would be interesting to know what percentage of Mr. Darwin's plants exhibited the new and constant characters and through how many generations his mutants were found to breed true, for then we could compare his results with those of investigators of our day. But his attention was centered upon the endeavor to find a cause

[52] "Life and Letters," 1886, Vol. III, p. 343.

for the abrupt variations and not on the formulation of laws of their action. Apparently he considered isolation to be the principal secondary cause or favoring condition, upon which view the obvious comment is that it requires no great stretch of imagination to conceive of similar isolation as occurring in nature and thus favoring mutation among uncultivated forms.

Having now hastily reviewed the oscillations in Darwin's opinions concerning the kinds, the causes and the laws of variation with relation to the origin of species, it is not my purpose to enter upon a discussion of the present-day mutation theory, which has grown out of a closer study, and a more scientific treatment, of the problems of variation and heredity than were attempted, or were perhaps possible in Darwin's time. It is desirable, however, to compare Darwin's views with generalizations from the mutation theory, which we can do, well enough for our present purpose, by merely recalling the seven laws which De Vries claims to be the logical outcome of his twenty years of cultural experiments upon plants. They are, with slight modifications as to wording and order, as follows:

1. New elementary species appear suddenly without intermediate steps.

2. New forms spring laterally from the main stem.

3. New elementary species attain their full constancy at once.

4. Some of the new strains are elementary species, while others are to be considered as retrograde varieties.

5. The same new species are produced in a large number of individuals.

6. Mutations take place in nearly all directions and are due to unknown causes.

7. Species and varieties have originated by mutation, but are, at present, not known to have originated in any other way.

Now, looking back over what Darwin wrote concerning variation, I can not believe that he would seriously have

disputed any of De Vries's propositions except the last. All would have had to stand or fall with that. He recognized the fact that new species had sometimes appeared suddenly without intermediate steps and that the new forms had sprung laterally from the main stem. I think he also substantially admitted that such new species attained their full constancy at once. As to the fourth affirmation of De Vries, with reference to elementary species and retrograde varieties, Darwin had no knowledge, for the distinction is original with De Vries. Darwin believed, as a general proposition, that "species are only strongly marked and permanent varieties, and that each species first existed as a variety,"[53] but, of course, in admitted cases of mutation this can not be true; and if Darwin had been obliged to concede De Vries's seventh proposition, the fourth might well have been allowed to go with it. The same is doubtless the case concerning De Vries's fifth law, which sets forth in effect that similar mutants are thrown off by many individuals of the same species at about the same time. As we have already seen, Mr. Darwin was convinced that if, for example, he were to admit the origin by mutation of a species of flying animal, for the reasons urged by Mr. Mivart, he would be compelled to assume "that many individuals varied simultaneously." I, therefore, do not see that he would have been interested, from a theoretical point of view, in disputing either of the two last-named declarations of De Vries except in connection with his seventh and last law, to which I shall presently refer. The sixth law of De Vries, which affirms that mutations take place in nearly all directions, is practically the equivalent of Darwin's first law that all organisms vary continually and in every part of their structure, provided it is agreed that mutations are only quantitatively different from Darwin's "individual variations," which was Darwin's own view. In so far as Darwin admitted the occurrence of mutation at all, he must have agreed that it could proceed in any

[53] "Origin of Species," 6th ed., 1882, p. 412.

direction. But now we come to the conclusion of De Vries which we know Darwin would not have accepted, at least in its entirety. As we have seen, he was compelled to concede that what we now call mutation had occasionally taken place and become the starting point of new races, but he was none the less unshaken in the conviction that this process was exceptional and extraordinary, and that, as a rule, a new species originated by the gradual building up of minute and even insignificant deviations from the average characters of an old species, which deviations we now call fluctuations. We know with what tenacity he held this view to the end of his life. For the doctrine of "insensible gradations," which touched mainly a minor premise in his general argument for evolution, Mr. Darwin was, unhappily, almost willing to relinquish the essence of the whole matter, which was his claim to the discovery of a *vera causa* in the evolutionary process. Notwithstanding the prior claim of Patrick Matthew, and the partial anticipation of Alfred R. Wallace and others, the establishment of the theory of natural selection was Mr. Darwin's most original and greatest achievement. Time has proved that he could have afforded to stand upon the general validity and applicability of this theory though every step in his argument in its favor had needed review and modification; for each passing year but adds to the impregnable mass of proofs by which it is affirmed and supported. Properly regarded, the mutation theory does not antagonize nor weaken the doctrine of natural selection—on the contrary, it merely offers itself as a helpful substitute for, or adjunct to, one of Darwin's subordinate steps in the approach to a consistent philosophy of the origin of species, leaving the last great cause of evolution as efficient as ever. It is, therefore, one of the tragedies of science that in this matter Darwin should have been ready to surrender his main position rather than to receive and to join forces with those who were coming to his aid, but whom he failed to recognize as friends.

JUVENILE KELPS AND THE RECAPITULATION THEORY. II

PROFESSOR ROBERT F. GREGGS

OHIO STATE UNIVERSITY

II. THE RECAPITULATION THEORY IN RELATION TO THE KELPS

ANY observations on juvenile kelps must call to mind the recapitulation theory. This theory, though applied both to animals and to plants, was built up exclusively on zoological evidence and has been amplified and discussed chiefly by zoologists. The reason is evident because of the definite proportions and structure of the animal body, the development of which must of necessity follow a very definite course, while among plants the body is of such loose and indefinite proportions that its development can seldom be rigidly described. But while the botanists have had very little to say about the recapitulation theory, they have always approved it and considered that it applied to plants just as truly, though not as conspicuously, as to animals.

It is somewhat surprising then to a botanist to find that this theory is being very vigorously attacked by some of the zoologists. One of the more recent papers is by Montgomery, who gives a review of the literature with a general discussion of the theory in his "Analysis of Racial Descent," 1906. In summing up he says (p. 193):

> Therefore we can only conclude that the embryogeny does not furnish any recapitulation of the phylogeny, not even a recapitulation marred at occasional points by secondary change. . . . An analysis of the stages during the life of one individual can in no way present a knowledge of its ancestry; and the method of comparing non-correspondent stages of two species is entirely wrong in principle.

And again at the close of the chapter, p. 203:

> The recapitulation hypothesis is scientifically untenable and where there has been transmutation of species, the embryogeny neither in

whole nor in part exactly parallels the racial history. The relation between them is always that of an inexact parallelism. Considerations based on any such idea of recapitulation are erroneous, and therefore of no help in determining racial descent.

In these sentences Montgomery is voicing not alone his individual opinion, but that of a very considerable school of embryologists.

The general tenor of these statements is scarcely open to question nor is the author's conclusion as to the worthlessness of the recapitulation theory. However, there is one word used in both the paragraphs quoted, though not in the portion of the first cited, that is unfortunate in that it is open to misunderstanding. It is the word exact. Exact has a certain mathematical flavor, which makes its application to living organisms difficult. Neither Montgomery nor any one else believes that there are anywhere two individuals, who are exactly alike in any respect whatever. We may fairly assume, that Montgomery means to say that there is no recapitulation of the racial history of the embryo sufficiently exact to aid in determining racial descent; and we shall so interpret his statements in the remainder of this paper.

A few years ago when the recapitulation theory was almost universally accepted one might have assumed that the noteworthy features of the development of the kelps were to be explained on that basis. But now in the face of such attacks on the theory no such assumption may be made. We shall therefore consider the development of the kelps in relation to the theory and to the criticism upon it in an effort to ascertain the real bearing of the foregoing observations.

It must be admitted that the juvenile forms of all the kelps are closely similar in a general way; but it does not necessarily follow that they are so because of any recapitulation of phylogeny. Such parallelism might be brought about by entirely different causes. This possibility has been perhaps most strongly urged by His, the eminent embryologist, who in a different way makes quite as

strong an attack on the theory as does Montgomery. In his "Unsere Körperform" as translated and quoted by Morgan ('03, p. 71) who does not, however, assent, His says:

> In the entire series of forms which a developing organism runs through, each form is the necessary antecedent step of the following. If the embryo is to reach the complicated end forms, it must pass, step by step, through the simpler ones. Each step of the series is the physiological consequence of the preceding stage and the necessary antecedent for the following. Jumps, or short cuts, of the developmental process, are unknown in the physiological process of development. If embryonic forms are the inevitable precedents of the mature forms, because the more complicated forms must pass through the simpler ones, we can understand the fact that paleontological forms are embryonal, because they have remained at the lower stage of development, and the present embryos must pass also through lower stages in order to reach the higher. But it is by no means necessary for the later, higher forms to pass through embryonal forms because their ancestors have once existed in this condition. To take a special case, suppose in the course of generations a species has increased its length of life gradually from one, two, three years to eighty years. The last animal would have had ancestors that lived for one year, two years, three years, etc., up to eighty years. But who would claim that because the final eighty years species must pass necessarily through one, two three years, etc., that it does so because its ancestors lived one year, two years, three years, etc.? The descent theory is correct in so far as it maintains that older, simpler forms have been the forefathers of later, complicated forms. In this case the resemblance of the older, simpler forms to the embryos of later forms is explained without assuming any law of inheritance whatever. The same resemblance between the older and simpler adult forms would remain intelligible were there no relation at all between them.

There are two ways of looking at this view of His's that every form is the necessary antecedent of the succeeding. These depend upon the length of stages considered. If we take stages separated by very small intervals of growth, His's contention must be true else there would be no continuity of development. But this is nothing more than a statement of the fact that all growth must be gradual and is no law of development. If instead of small intervals we take the whole development, the statement

would become: "The developmental stages of an organism are only the physiologically necessary steps for the formation of its adult body from its earliest stage, which is in most cases the egg." This is definite and it can be readily tested by the facts, while the other is so vague as to be scarcely susceptible of any such test. There is no middle ground between these two alternative interpretations of the statement. For if an organism is found to which it will not apply if somewhat but not greatly separated stages be considered, all that is necessary is to take shorter and shorter stages until finally any ontogeny must conform to it.

Let us apply then, His's view, thus interpreted, to the kelps. We have so far confined the account to the external morphology and have said little about their histology. This will be of interest here. The general plan of structure is the same in both stipe and lamina and similar in all kelps. Within the epidermis is the cortex composed of polygonal or rounded cells which may be thickened and hardened to form strengthening tissue. Within this is a pithweb made up of irregularly interlacing filaments which sometimes show very remarkable differentiation. Oliver ('87) first worked out in detail, showing that in Macrocystis and Nereocystis, especially, sieve tubes are developed which form a regular zone of vertical vessels around the less differentiated center of the pith. The sieve plates of these become obliterated by the formation of callus as in the spermatophytes. There is good reason to believe that they are efficient in the transfer of materials from one part of the plant to another and their possession may have made it possible for these plants to attain the great lengths they sometimes reach. The simpler internal pith consists of interlacing branching hyphae which run in all directions. Many of these meet and at their junctions develop sieve plates connecting them with one another, at the same time becoming swollen at the ends like the flare of a trumpet. Such trumpet hyphae are common in most members of the Laminariaceae. In Ren-

frewia, however, the pith consists of only moderately elongated cells which interlace somewhat as in other kelps, but very much less conspiciously. The majority of them are not longitudinal, but transverse in their general course, so that a cross section shows more of them cut lengthwise than a longitudinal (see figures, Griggs, '06). Scarcely any of them are sufficiently elongated to merit the name of hyphæ. Very few give indications of developing into trumpet hyphæ. It is evident that Renfrewia presents a transition from a pithweb of simple polygonal cells to the complex differentiation of the higher kelps such as Nereocystis. Such plants must of necessity pass through the condition of Renfrewia in order to attain mature structure. We have here then a perfect illustration of the truth of His's idea—save in one respect. His contends that the developmental stages are *only* the necessary morphological precursers of the adult. But in this case they may be phylogenetic recapitulations also. There is nothing in the evidence so far to prevent a decision either way.

Let us consider some other features of the development. All of the young forms pass through a period when the stipe is short as compared with the lamina. In all which have been described above except Hedophyllum, this condition persists until a certain very definite period, after which the stipe elongates rapidly (see figures of Egregia). This condition is so similar to the adult stage of Renfrewia that one is tempted to consider it a recapitulation of such a stage. But instead it may be only a necessary physiological adaptation which the young plant undergoes early in its development in order to provide a large photosynthetic area to furnish the food necessary for rapid growth. *A priori* this would seem a reasonable interpretation of the facts and it may be that we should consider them without other significance. It is, however, difficult to believe that the simple Renfrewioid form is the necessary precurser of adult forms so diverse as Postelsia and Egregia, Eisenia and

Nereocystis, Thallasiophyllum and Macrocystis. One might imagine other forms upon which each of these might have been built up more directly than on this one. This is particularly true in the case of Egregia and Hedophyllum, where, while the young are indistinguishable, the course of development is diametrically opposed. Egregia dwarfs the lamina and becomes nearly all stipe; Hedophyllum obliterates the stipe and becomes a sessile lamina. If ontogeny represents merely stages physiologically necessary to the attainment of the adult form, why should Hedophyllum produce a stipe at all?

Similar conditions are presented by very many other cases, especially among animals where some organ is developed in the embryo which later disappears without being of service either to the embryo or to the adult. Such cases have in the past been the main evidence brought forward for the recapitulation theory, as it has been supposed they were explicable only on the basis of a recapitulation of the phylogeny. Familiar examples are cited by Morgan (see below), and many more might be added.

Not all who attack the recapitulation theory go so far as to discard it altogether. Many recognize in it a truth and seek to modify it to fit certain facts. The form which has the largest number of adherents is perhaps that proposed by Morgan ('03), who believes that animals in their ontogeny repeat not the adult, but the embryonic stages of their ancestors; that the presence of a certain structure in the embryo means that the ancestors of the species to which the organism belongs had similar embryonic stages. This he calls the "Repetition Theory." Much of the evidence which the zoologists bring forward in favor of such a modification as against any broader application is so conclusive, one must acknowledge that such is a correct statement of the facts in the particular cases cited, whatever the general law of development may be. Morgan calls attention to the fact that the gill-clefts and the notochord, structures on

the recurrence of which the recapitulation theory was largely built, appear just as early in the embryo of the fish and of Amphioxus, respectively, as in that of a mammal. He cites the case of the baleen whale which forms teeth in the embryo like any other mammal, but these beginnings, instead of continuing their development, are absorbed and do not even pierce the gums. The same is true of the dental ridges of birds, where teeth begin to form but soon disappear.

The evidence presented by the kelps clearly tends to establish this repetition theory of Morgan. The juvenile forms of the plants have so many points in common that there can be scant doubt but that their ancestors had similar juvenile forms. It must be added here also that those plants whose development we have traced above are not special cases, but are only illustrations of the facts common to all kelps. The writer has in his possession full series of several genera which have never been described at length. These and all others which have been worked out follow the same course of development. Among those upon which fairly complete published data are available, may be mentioned: Agarum, Barber, '89; Alaria, Schrader, '03, and others; Cymathere, Griggs, '07; Eisenia, Setchell, '96b, '05a; Lessonia, Reinke, '03; Nereocystis, MacMillan, '99; Pterygophora, MacMillan, '02; Saccorhiza, Barber, '89; Thallasiophyllum, Setchell, '05a.

If we may consider the repetition theory established how much will it help us with our phylogenetic problem? Why should widely diverse forms have ancestors with similar embryos? How were these similar stages acquired and why do they persist? They must be meaningless so far as phylogeny is concerned, except as they are considered as stages which once led to the development in the adult of the structures which they represent. But why should embryonic characters persist and not adult ones? Is there any line of demarkation between embryo and adult beyond which the action of heredity changes?

Leaving these questions for the present, we may examine the facts in the development of our kelps, to ascertain whether these juvenile forms repeat only other juvenile forms or whether they go farther and approximate the adults of their ancestors. Nothing could be more instructive on this point than the figure of the young plant of Lessoniopsis printed beside the adults of Renfrewia (Figs. 15-17). In all external characters save the characteristic spots of Lessoniopsis and the reproductive maturity of Renfrewia they are in essentials identical. The structure of the holdfast is particularly interesting. Both are simple discs strengthened by primary hapteres originating through the uneven growth of the disc itself. The young of other kelps might have been used for this comparison, *e. g.*, Hedophyllum (cf. Fig. 6), but Lessoniopsis retains these primitive characters at a larger size than the others and therefore lends itself more easily to photography while its determination is at the same time certain because of the spotted lamina. In Pterygophora the correspondence is in all respects just as complete, see MacMillan's figures ('02). There persists for a considerable period the simple lamina with the short stipe on the primitive disc and its primary hapteres for holdfast. After the secondary hapteres have appeared and until the midrib has been formed the young plants are very difficult to distinguish from those of *Laminaria saccharina* which grows in the same locality. These again are in all respects, except size and reproductive maturity, like the adult plants of their species.

It seems obvious that we can not well consider these facts without comparing these non-correspondent stages of Lessoniopsis and Renfrewia, and of Pterygophora and Renfrewia and Laminaria. The simple facts of the case are that Lessoniopsis and the others when still very small pass through a condition which must be considered within the generic limits of Renfrewia. Conversely, the adults of Renfrewia do not differ in any important char-

acters save size and reductive maturity from the young of the other kelps which have been studied. But Renfrewia, juvenile or adult, is not one of the ancestors of these higher kelps. It is only a simpler form which we take to have been left behind in the evolution of the kelps. Our actual knowledge of their ancestors is almost nothing. But if we were to reconstruct a generalized common ancestor for the kelps, by projecting backward, from the different tribes, lines indicating their apparent course of evolution, until they converged and met, we should have to conceive a plant very similar in all respects to Renfrewia.

What then is to be said concerning structures which do not recapitulate adult but only embryonic conditions? In the toothless animals, the whale and the bird, the development of teeth in the jaw is entirely unnecessary, as has been pointed out in considering His's idea. It may even be said to hinder the attainment of the adult condition. The same is true of the mammalian gill-slits and of most of the structures which have in the past attracted attention in connection with the recapitulation theory. As the ancestral period, when such structures were fully developed in the adult, becomes more and more remote, the tendency to inherit them becomes less and less, because of the cumulative impulses given to the heritage by the nearer ancestors. Consequently, they are successively less and less developed. Any gradual loss of inherited structures can, in the nature of the case, take place only from the mature condition backward towards the beginning of the life cycle; otherwise we should have adult structures with no ontogenetic history. Therefore we can understand why it is that in many cases only the embryonic stages of ancestral organs persist in the ontogeny.[3]

[3] The cutting off of end stages in the development of organs has given rise to the idea that the adult stages are "pushed back into the embryo." Such a misconception easily arose from the loose language in which the facts have often been expressed. Conklin ('05) has rightly pointed out its incorrectness.

Thus the embryogeny will be gradually shortened by the omission of more and more of the superfluous ancestral stages; and it will tend finally to retain only such stages as are necessary to the attainment of the adult form. It will be noted that this is the view of His, which thus becomes a statement of an inevitable tendency in development, which is very different from a complete law of embryogeny. Though life cycles may approach very closely such a limiting condition, it is doubtful if they would ever completely realize it.

Besides changes in ontogenies brought about by the cutting off of end stages no longer used there is another source of change. This is secondary adaptation. It is on this point that Montgomery largely makes his case, insisting that organisms are as subject to change in one period of their life cycles as another. In this matter also we must agree that secondary changes are sometimes very evident and conspicuous—probably more so among animals than plants. The fetal membranes are very familiar examples of such secondary adaptations. But though they are much modified the fact must not be lost sight of that they are in part at least adaptations of previously existing organs with different functions and not new structures. Not only may an embryo adapt itself to its conditions; it may simulate other forms; or interpolate stages; or become otherwise modified as the species undergoes transmutation. Yet the important point to consider is not that a few have done this, but that the great majority have not falsified their heritage beyond all recognition, that they still persist in spite of changed conditions and secondary adaptation in preserving so many indications of their ancestry.

Montgomery considers this matter of secondary change so weighty, not because of a great amount of observation brought forth, but for logical reasons. He holds that:

> The egg of a mammal is as dissimilar from that of a fish as their adult stages, no matter whether their differences are perceptible or not. This was the idea of the great old master Von Baer: The egg is as much a bird as is the hen.

Although perfectly true in a physiological sense, this is incorrect in this connection. Potentially the egg of one animal is as different from that of another as their adult forms, but morphologically they correspond. Morphology is not concerned with the "growth energies" of organisms, but only with their form and structure. A similar mistake was made by His in the quotation cited above, where he takes for an illustration of his views an animal which had lengthened its life over that of its ancestors. The logical deduction from such an example under the recapitulation theory would be that the last form should *die* at the end of each period, one, two, three years, etc., in order to recapitulate its ancestry, rather than that it *lives* one, two, three years to do so. The absurdity of this lies in the fact that length of days is not a morphological character. The recapitulation theory has nothing to do with physiology; it is purely a matter of morphology.

The degree of approximation between the young of a higher form and the adult of a present-day lower form of the same line depends upon the degree of specialization and divergence of the lower species from the main path of descent. It is usually recognized that most of the lowest and morphologically simplest organisms are highly specialized for some particular mode of life more or less different from the ancestral. This specialization nearly always carries with it some structural adaptations, but these may not obscure the ancestral characters. Thus Marchantia has evolved a chambered thallus highly differentiated, to adapt it at once to an aquatic substratum and aerial life, but it still retains a sporophyte perhaps very similar in some features to that of the ancestors of the higher plants at the liverwort stage. On the other hand, organisms are occasionally found which give every indication of being primitive. These are truly forms with arrested evolution. Renfrewia is an example; Anthoceros is another, less free from specialization but contrasting strongly

with Marchantia. Such primitive types are few and far between for obvious reasons: if an entire group advances rapidly it moves up bodily into a higher plane and leaves behind only such forms as stray into some byway of specialization, which specialization would be a bar to future progress except in the line upon which the form had entered. All unspecialized forms left behind in the advance of the race are likely to be displaced early in the struggle for existence because of their lack of particular adaptations. It is accordingly only in such environments as present no specialized demands upon their inhabitants that we may expect to find these primitive forms and it will be observed that to a large extent such is the case.

Wherever a form is found with simple unspecialized structure it becomes at once a problem to decide whether it is in reality primitive or a degenerate type. If there is no paleontological history to aid in the solution a conclusive answer to this question is often impossible. However, unless there is definite evidence of degeneration in vestigial structures or the like, as there is in many cases, for example the mistletoes; it is generally safe to assume that the present condition of the organism represents its highest attainment in the process of evolution. Degenerate forms usually manifest a high degree of fixity in their organizations and great variability is seldom found in such forms. It might be suggested that the apparently primitive structure of Renfrewia may be due to degeneration from a condition more highly differentiated. It possesses, however, no vestigial or unused organs, with the exception of the basal cone of the stipe. Every portion of the plant is functional. There are no peculiarities about its structure which mark it as different from the other kelps. On the contrary, its reproduction and its histology are similar to them. Its habitat, quiet water just below the tide mark, is exactly that which would be expected of the ancestors of the kelps before they acquired adaptations enabling them to endure the

heavy surf and the drying incident to living above the tide mark. At the same time it has such a high degree of variability in its whole structure that it is difficult to pick out characters sufficiently fixed to be of use in describing it. There seems to be no good reason to doubt its primitive position.

Taking all the evidence into consideration, it seems to the writer that we are bound to conclude that though organisms are subject to adaptation at any stage of their life cycles and may gradually cut out superfluous stages, yet, except as some such tendency has operated to change the heritage, the development of the individual does recapitulate the history of the race. The degree of correspondence of any individual cycle with its ancestral history is various in different cases but may be very close. Recapitulation must take place if there is any force which tends to make offspring like parent, if heredity is of any importance in moulding the forms of organisms. On the other hand, if there be any variability or transmutation of individuals in stages other than the adult end stages of their life cycles, the recapitulation can not be perfect, but must be marred at every stage where secondary change has taken place. The extent to which any individual will recapitulate its phylogeny must therefore depend on the balance maintained between these two forces in the given case. The value of a study of ontogeny for the taxonomist or phylogenist will depend altogether on the facts of the special case. In each case the evidence must be weighed before a conclusion can be reached. Ontogeny may be of greater or less worth in the attempt to build a rational system of nature. But variable as its utility may be in different cases, the recapitulation theory states a fundamental law of a tenddency of the embryogeny and must be considered as one of the several interacting tendencies which together control the development of animals and plants.

COLUMBUS, O., August, 1908.

LITERATURE

No attempt is here made to list the voluminous literature devoted to discussions of the recapitulation theory. The more important papers have been thoroughly listed and summarized in many of the standard general works, *e. g.*, Montgomery.

Barber, C. A. On the Structure and Development of the Bulb in *Laminaria bulbosa*. *Ann. Bot.*, 3, 41. 1899.

Conklin, E. G. The Organization and Cell Lineage of the Ascidian Egg. *Jour. Acad. Nat. Sci. Philadelphia*, vol. 13. 1905.

Frye, T. C. *Nereocystis lutkeneana*. *Bot. Gaz.*, 42, 143–146, fig. 1. 1906.

Gepp, A. and E. S. *Lessonia grandifolia*. *Jour. Bot.*, 43, 2. 1905.

Grabendörfer. Zur Kenntnis der Tange. *Bot. Zeit.*, vol. 43. 1885.

Griggs, R. F. *Renfrewia parvula*, New Kelp from Vancouver Island. *Postelsia*, 1906, 247–274, pls. 16–19. 1906.

———. Cymathere, a Kelp from the Western Coast. *O. Nat.*, 7, 89–96, pl. 7, fig. 1. 1907.

Hooker, J. D. Flora Antarctica, 2, t. 171, 167. 1844.

Humphrey, J. E. On the Anatomy and Devolpment of *Agarum turneri*. *Proc. Am. Acad.*, 23, 201. 1886.

Kjellman, F. R. Laminariaceæ in Pflanzenfamilien, 1², 242–260. 1893.

MacMillan, C. Observations on Nereocystis. *Bull. Torr. Club*, 26, 273–296, pls. 361–362. 1899.

———. Observations on Lessonia. *Bot. Gaz.*, 30, 318–334, pls. 19–20. 1900.

———. The Kelps of Juan de Fuca. *Postelsia*, 1901, 193–220, pls. 22–26. 1901.

———. Observations on Pterygophora. *Minn. Bot. Stud.*, 2, 723–741, pls. 57–62. 1902.

Montgomery, T. H. The Analysis of Racial Descent in Animals. New York. 1906.

Morgan, T. H. Evolution and Adaptation. New York. 1903.

Oliver, F. W. On the Obliteration of the sieve tubes in the *Laminariæ*. *Ann. Bot.*, 1, 95. 1887.

Postels and Ruprecht. Illustrationes algarum. 1840.

Ramaley, Francis. Observations on *Egregia Menziesii*. *Minn. Bot. Stud.*, 3, 1–9, pl. 1–4. 1903.

Reinke, J. Studien zur vergleichende Entwickelungsgeschichte der Laminariaceen. Kiel. 1903.

Saunders, D. A. Algæ of the Harriman Alaska Expedition. *Proc. Wash. Acad. Sci.*, 3, 391–486, pls. 18–62. 1901.

Schrader, Herman F. Observations on *Alaria nana*. *Minn. Bot. Stud.*, 3, 157–166, pl. 23–26. 1903.

Setchell, W. A. Concerning the Life History of *Saccorhiza dermatodea*. *Proc. Am. Acad.*, 26, 177–217, pls. 1 and 2. 1891.

———. Classification and Geographical Distribution of the Laminariaceæ. *Trans. Conn. Acad.*, 9, 333–375. 1893.

———. Notes on Kelps. *Erythrea*, 4, 41–48, pl. 1. 1896a.

———. *Eisenia arborea*. *Erythrea*, 4, 129–133, pl. 4; 155–162, pl. 5. 1896b.

———. The Elk Kelp. *Erythrea*, 4, 179–184, pl. 7. 1896c.
———. *Laminaria sessilis* in California. *Erythrea*, 5, 98. 1897.
———. Notes on Algæ, I. *Zoe*, 5, 121–129. 1901.
———. Post Embryonal Stages of Laminariaceæ. *Univ. Cal. Pub. Bot.*, 2, 115–138, pls. 13–14. 1905a.
———. Regeneration among Kelps. *Ibid.*, pp. 139–168, pls. 15–17. 1905b.
———. Nereocystis and Pelagophycus. *Bot. Gaz.*, 45, 125. 1908a.
———. Critical Notes on the Laminariaceæ Nuov Notarisia 19: 90–101. *Rev. Jour. Roy. Mic. Soc.*, 1908, 474. 1908b.
Setchell, W. A., and Gardiner, N. L. Algæ of Northwestern North America. *Univ. Cal. Pub. Bot.*, 1, 165–418, pls. 17–27. 1903.
Sykes, Miss M. G. Anatomy and Histology of Macrocystis and *Laminaria saccharina*. *Ann. Bot.*, 22, 291–325, pls. 19–21. 1908.
Thuret. Recherches sur les Zoospores des Algues et les Antheridies des Cryptogames. *Ann. Sci. Nat.*, ser. 3, 14, 240, t. 30. 1850.
DeToni, J. B. Sylloge Algarum, 3, 316–374. 1895.
Wille, N. Beitr. Physiolog. Anatomie Laminariaceanum. *Univ. Fests. til. K. M. K. Oskar*, II, Anleidung Regjieringsjubilaeet. 1897.
Williams, J. L. Germination of the Zoospore in Laminariaceæ. *Nature*, 62, 613. 1900.
Yendo, K. On Eisenia and Ecklonia. *Bot. Mag. Tokyo*, 16, 203. 1902.
———. Two new Marine Algæ from Japan. *Ibid.*, 17, 99–104, pls. 2 and 3. 1903a.
———. Hedophyllum spirale sp. nov. *Ibid.*, 17, 165–173, pl. 6. 1903b.

NOTES AND LITERATURE

PLANT PHYLOGENY

The Origin of the Archegoniates.—There is in the theoretical discussion of plant evolution perhaps no gap which is more difficult to bridge than that between the thallophytes and the archegoniates, or more precisely that between the higher algæ and the liverworts, mosses and ferns. The most recent discussion of this problem is by Schenck,[1] one of the authors of the "Lehrbuch der Botanik," who is convinced that the archegoniates arose from the Phæophyceæ or brown algæ.

A number of earlier writers have endeavored to relate the archegoniates to the Chlorophyceæ or green algæ. This has generally been attempted through Coleochæte or Chara. Coleochæte has been a favorite type for the reason that its fruit, derived from the germination of the egg, is a globular multicellular structure somewhat resembling the sporophytes of the simpler liverworts in the order Ricciales. Allen, however, has reported that the phenomenon of chromosome reduction takes place during the germination of the egg and not at the end of this period of fructification, which clearly indicates that the latter development is not the homologue of a sporophyte. A comparison of the sexual organs of Coleochæte with those of the archegoniates presents further difficulties, for the antheridia and oogonia of Coleochæte are unicellular structures very different from the multicellular sexual organs of the archegoniates. The general morphology of Chara is somewhat moss-like, but in this form also the life history fails to present any evidence of an alternation of generations comparable to that of the archegoniates. Furthermore, the essentially unicellular structure of the oogonium (the protective investment of which is clearly a secondary feature) bears no fundamental resemblance to an archegonium, and its remarkable antheridium is unique among the sexual organs of plants.

The Rhodophyceæ or red algæ have a highly developed sporophytic phase, but their diverse morphology as well as that of the

[1] Schenck, H. Ueber die Phylogenie der Archegoniaten und der Characeen. *Engler's Botan. Jahrbuchern.*, XLII, 1908.

gametophyte is so very different from anything present in the lower achegoniates that relationships between the two groups seem hardly possible. The work of Yamanouchi on Polysiphonia clearly indicates that the tetraspore mother cell when present is the seat of reduction mitoses terminating the sporophytic phase of the typical life history of the higher red algæ. The sexual organs of the red algæ are also far removed in structure from the sexual organs of the achegoniates.

Davis in 1903 first pointed out the resemblance of the achegonium and antheridium of the bryophytes to the plurilocular sporangium or gametangium of the brown algæ, and advanced the view that the former arose from such a type of sexual organ as the latter through the differentiation of a sterile protective envelope around the gametes (in response to terrestrial life habits), and such sexual evolution as would give the highly developed condition of heterogamy present in the archegoniates. Davis, however, was unwilling to concede the probability of an origin of the archegoniates from the brown algæ because of the great morphological differences between the two groups, but suggested that there may have been forms of green algæ with plurilocular sporangia, now extinct, from which the bryophytes have been derived.

Schenck accepts the view of Davis that the sexual organs of the archegoniates are homologous with plurilocular gametangia and derived from them, but argues for a direct origin of the archegoniates from the brown algæ. He gives an excellent series of figures, selected from various authors, which illustrates the principal forms of plurilocular sporangia and gametangia of the brown algæ, and presents a similar series of figures of antheridia and archegonia of bryophytes and pteridophytes showing various points of resemblance in their structure and development. The resemblances are easily followed between the gametangia of the lower brown algæ (Phæosporeæ) and the sexual organs of mosses and most liverworts. However, there are difficulties when the antheridia and oogonia of Dictyota, the endogenous antheridia and sunken archegonia of Anthoceros, and the sunken sexual organs of certain eusporangiate pteridophytes, Lycopodium, Selaginella, Isoetes, etc., are compared with plurilocular gametangia of brown algæ in an attempt to derive in a direct manner the former from the latter. The reviewer agrees with Schenck that plurilocular sporangia and gametangia of the brown algæ are in the same class of repro-

ductive organs with archegonia and antheridia, but would not be willing to go so far as to hold that the latter have been derived directly from the former.

There follows then in Schenck's paper an attempt to homologize the spore mother cell of the archegoniates with the tetrasporangium of the Dictyotaceæ, based on the fact that the mitoses in both cells are reduction divisions terminating the sporophytic phases of life histories with an alternation of generations. The endogenous formation of spore mother cells in the archegoniates is regarded as an ecological adaptation associated with terrestrial life habits. The analogy is perfectly clear, but it may well be questioned whether it suggests so close a relationship as to justify an homology, especially since reduction phenomena are now known for a number of unrelated groups of algæ and fungi. The tetraspore mother cell of the red algæ is probably in most forms also the seat of chromosome reduction terminating a sporophytic phase. The mitoses in the zygote of Spirogyra have recently been shown by Karsten to be reduction divisions, as has been suspected, and it is altogether probable that similar reduction mitoses will be found to occur with the germination of the eggs of Œdogonium and a number of other algæ, and for certain phycomycetes as well. All of these cells in being the seat of reduction mitoses are analogous to the spore mother cells of archegoniates, but that would not warrant their being considered as homologous with the latter structures. There is, on the contrary, good reason to believe that in plants reduction phenomena became established as features in the life histories of a number of groups quite independently of one another, as the evidence indicates was also true of the processes of sexual evolution and the differentiation of sporophyte generations. Chromosome reduction as a physiological process seems to be a corollary of sexual nuclear fusions, but the cells concerned in the former are less likely to be homologous with one another than the cells concerned in the latter, since they are a part of a new phase which tends to become elaborated as the intercalated sporophytic generation. It is clear that a number of types of gametes throughout the plant kingdom are not homologous, and equally clear that several different forms of cells associated with chromosome reduction are not homologous.

Finally, Schenck compares the gametophytes and sporophytes of the archegoniates with the thalli of the brown algæ, but it is doubtful whether he really strengthens his case. The resemblance of the gametophytes of thallose liverworts to band-shaped

forms of the brown algæ is but superficial and does not extend to fundamental anatomical features. Indeed, both the brown algæ and the bryophytes present so remarkable a variety of vegetative structure that it is very difficult to pick out types which may be held to be representative of the two groups. Schenck refers frequently to the conditions in the Dictyotales, but this assemblage is very far from being representative of the brown algæ as a whole and stands rather as a group of very uncertain relationships. The simpler gametophytes of the pteridophytes may more readily be compared to the thalli of some of the lower brown algæ, but they are very different from the higher forms where the sexual conditions are those of heterogamy, and, moreover, this simplicity in some types of pteridophytes is rather evidence of that general principle of plant evolution according to which the gametophytes become reduced in structure as the sporophytes attain higher levels of complexity. It is of course much more difficult to make comparisons between the sporophytes of the achegoniates and the thalli of the brown algæ.

This portion of Schenck's paper appears to the reviewer to give very little support to his speculation and herein lies its principal weakness, for if the vegetative morphology of the brown algæ is not suggestive of relationships to the archegoniates the resemblance between their sexual organs can scarcely alone carry much force, especially since the latter may with great probability be supposed to refer to older and more primitive conditions. The reviewer is still inclined to his opinion that there have probably existed groups of the green algæ now extinct, the sexual organs of which were plurilocular gametangia, from which the archegoniates may have arisen. We have at present suggestions of such types in Schizomeris, *Stigeoclonium tenue irregulare* and conditions occasionally found in Draparnaldia and Chaetophora. That such groups of extinct green algæ may have originally had close relationships to the brown algæ is quite possible.

In the last section of this paper Schenck discusses the origin of the Charales. Of especial interest is the suggestion that the puzzling antheridium of this group may be interpreted as a sorus of antheridial filaments developing endogenously and may be compared to the sori of plurilocular sporangia which are produced externally on the surface of certain brown algæ. According to this view the globular male organ of the Charales is really

a complex of eight clusters of true antheridia in the form of filaments, and the entire structure constitutes a sorus-like structure in which the antheridial filaments arise endogenously. This conception has strong support in the abnormal conditions described by Ernst for *Chara syncarpa* where antheridial filaments were found developing externally from cells below the oogonium giving an hermaphrodite association of sexual organs. Schenck considers the Charales to be much more closely related to the brown algæ than to the green, basing his views on the above considerations together with certain resemblances between their vegetative structure (characterized by nodal and internodal regions) and that of certain brown algæ, Spermatochnus, Desmarestia, etc.

BRADLEY M. DAVIS.

HOLOTHURIANS

Clark's The Apodous Holothurians.[1]—Revisions of genera and larger groups require more painstaking care and research than most other forms of biological study, certain current opinion to the contrary, notwithstanding. Dr. Clark's memoir is a good example of a revision applied to a difficult group of animals. It is a well-executed and well-matured piece of work, and one which fulfills all reasonable expectations. It is easily the most important treatise that has ever been published upon the families Molpadiidæ and Synaptidæ.

The monograph is based upon a critical examination of about 2,200 specimens in the collection of the National Museum, and is divided into four parts. The classification of the two families is first discussed and a table of accepted genera, with type species, is given. Part II is an annotated list of the species in the collection of the National Museum, including descriptions of new genera and species. Part III contains an account of the Synaptidæ, their morphology, embryology, physiology, ecology and taxology, with keys to genera and species, and a short notice of each species, special attention being given to the geographical distribution. In Part IV, the Molpadiidæ are treated in a similar manner. Of the thirteen plates, three are

[1] The Apodous Holothurians, A Monograph of the Synaptidæ and Molpadiidæ, Including a Report on the Representatives of these Families in the Collections of the United States National Museum. By Hubert Lyman Clark. Smithsonian Contributions to Knowledge, Part of Vol. XXXV, 231 pp., XIII plates, 1907 (issued early in 1908).

in color. The figures are intended to illustrate not only the new forms described, but also previously known species that have not been figured and some others, figures of which will be of service to the student. In a number of instances the nomenclature has been changed, and has been placed on as firm a basis as possible by the use of the generally accepted principles of the International Code. It will be seen that the monograph has a wider scope than a systematic revision, including as it does accounts of the anatomy, embryology and physiology.

The interesting account of the history of the classification of the two families is followed by an important consideration of the characters used in classification, and a discussion of the subfamilies and leading genera. Twenty-nine genera, of which 8 are new, are accepted, distributed as follows: Synaptinæ, 11 genera (2 new) comprising 60 species; Chiridotinæ, 7 genera (3 new) with 22 species; Myriotrochinæ, 3 genera, 6 species; Molpadiidæ, 8 genera (3 new and 1 new name) with 46 species. Dr. Clark has discovered that Ankyroderma is practically a juvenile condition of Trochostoma. As generally defined the former is distinguished from the latter by the presence of rosettes of racquet-shaped rods from the center of which there extends outward a conspicuous anchor. It was found, from a study of more than 350 specimens of these two genera, that the presence of anchors and rosettes of racquet-shaped rods can not be regarded as even a constant specific character. For example, small specimens of *Trochostoma intermedium* Ludwig with very thin skin are clearly Ankyroderma. Large specimens have a rather thick body wall and very numerous deep red or brown bodies in the skin, but no rosettes. The rosettes disintegrate into heaps of rounded colored bodies which differ from calcareous plates or particles in being chiefly phosphoric acid and iron. They are therefore quite unlike the ordinary calcerous deposits of holothurians, and are named "phosphatic deposits."

"As to the significance of these facts our knowledge is as yet too imperfect to draw any clear conclusions. Chemical analysis[2] of the

[2] The composition of these bodies is given as $FePO_3 + 4H_2O = 66.2$, $Fe(OH)_3 = 20.2$ and $CaCO_3 = 6.4$. There is also probably Mg present. "There is also reason to believe that the amount of $CaCO_3$ is subject to much variation; probably when calcareous particles are first transformed into colored bodies, $CaCO_3$ is the most important substance present, and

deposits shows that the colored bodies are radically different from the ordinary deposits in the skin. Both are possibly connected with the process of excretion; but why one should replace the other it is certainly hard to say. That the change is closely connected with the age of the individual seems to me almost certain, though it must be remembered that size in echinoderms is not a sure criterion of age. It is interesting to note that most of the species of Ankyroderma described have been less than 60 mm., while many of the Trochostomas range over 75" (p. 19).

The name Trochostoma antedates Ankyroderma, but both are synonyms of Cuvier's Molpadia (1817) which includes also Haplodactyla Grube (not Semper), as well as the long-discarded Embolus Selenka, and Liosoma Stimpson (not Brandt). In this enlarged genus Molpadia, twenty-seven species are recognized.

Some of the more important changes in the limits or names of genera, as well as certain new genera, will be noted. Synapta is monotypic and restricted to *S. maculata* Chamisso and Eysenhardt (*S. beselii* authors); Oestergren's Chondroclœa is called by the older name Synaptula: Leptosynapta Verrill is reinstated for the *inhærens* group; *Synapta kefersteinii* is made the type of a new genus Polyplectana; the recently described Opheodesoma is accepted for the *Euapta glabra* group; the old species *Chiridota rufescens* is made the type of a new genus Polycheira: Taeniogyrus Semper, for *Chiridota australiana* Stimpson, is accepted as distinct from the later Trochodota Ludwig: *Chiridota japanica* v. Marenzeller is made the type of Scolidota, new; Achirodota is founded upon *Anapta inermis* Fisher, and Toxodora Verrill is reinstated. The most important change in the Molpadiidæ has already been noted. Haplodactyla Semper 1868 (not Grube, 1840) is renamed Aphelodactyla, with five species. Ceraplectana and Himasthlephora are two new genera, the former near Molpadia, the latter related to Gephyrothuria Koehler and Vaney.

It has occurred to the present reviewer that, had space permitted, a very useful feature would have been the insertion of a complete diagnosis under each species not described in Part II. It is not possible to include in keys all the positive characters of a species, nor is it always possible for the average

as the color deepens, it decreases rapidly in amount. Apparently the calcium as well as the CO_2 is excreted as these changes take place" (p. 143). The presence of phosphatic deposits is limited to the Molpadiidæ among echinoderms.

student to have access to original descriptions. No one is able to tell when an apparently useless character (from the systematist's standpoint) and therefore one invariably omitted from keys, may not assume prime importance in the light of unnamed material. The practical difficulty that one has in depending upon literature and concise revisions is this. By testimony of keys (and figures too) one may have a species very close to a named species, yet there may be present in the questionable form additional characters of which no mention is made in keys. If one has not access to the original or some later authentic description he is "up a stump." The writer has so often found himself in this undesirable position that he speaks with some feeling on the subject.

However, the lack of descriptions is partly compensated for by the excellent notes under "Remarks," and in some cases by the republication of figures. Students of the group have every reason to be grateful to Dr. Clark for a very timely and useful memoir, and one which has in several instances reduced to order what was seemingly hopeless chaos.

W. K. FISHER.

LEPIDOPTERA

The Blue Butterflies of the Genus Celastrina.—In the second volume of Mr. J. W. Tutt's "British Butterflies," recently published, is a most exhaustive account of the small blue butterflies represented in Europe by *Celastrina* (vel *Cyaniris*, vel *Lycæna*) *argiolus*, and in America by the common and widely distributed *C. pseudargiolus*. The latter insect has long attracted much attention, owing to its remarkable polymorphism, which has been elucidated very fully by Edwards and Scudder. Mr. Tutt has gone over the whole subject afresh, and with the assistance of Dr. T. A. Chapman and Mr. G. T. Bethune-Baker, has been able to reach a number of very interesting conclusions. It appears that Celastrina is essentially an old world type; found, or represented by close allies, in every one of the great zoological regions of the Eastern Hemisphere, though feebly represented in Australia and Africa. In America, it is represented by *C. pseudargiolus* and its subspecies, one of which extends as far south as Panama. An examination of the structural characters, especially the genitalia, shows that *pseudargiolus* is not in any way definitely separable from the palæarctic *argiolus*, of which it must be considered a geographical race. It appears probable

that *C. argiolus* reached America in late Miocene times, and being able to live on a great variety of plants, spread widely, producing various local races. So long as it was restricted to temperate regions, it did not come to differ radically from the old world type; but the form *gozora* Boisduval, of the mountains of Mexico and Central America, is very striking in appearance. Even this last, however, has the genitalia and other structures of genuine *argiolus*. This case is especially instructive, because it indicates that an insect may spread very widely, invading regions with exceedingly diverse climates, and yet not change materially in the characters of the genitalic armature. When we remember how frequently allied species of insects, inhabiting the same or similar regions, are separable by genitalic characters, it seems that these are little or not at all connected with obvious environmental factors. To say that genitalic modifications are due to "mutation" does not really explain them; it remains to be shown, if that is possible, what it is that breaks down an established genitalic type, giving rise to new forms which rank as species. In the case of *Celastrina*, it is not to be assumed that its structural features are so immobile that they are incapable of modification. As a matter of fact, the numerous old world species are distinguished by the possession of very distinct genitalia, each very constant within specific limits. In Asia there are very distinct races, having precisely the structure of *C. argiolus*, and at the same time species exceedingly like *argiolus* superficially, but quite different in their genitalic appendages. From the standpoint of the natural selectionist, it may be remarked that there was nothing to be gained by genitalic differentiation in America, so long as only one species of Celastrina inhabited the country; and further, that the range of the insect, with all its local modifications, was practically continuous. It may be that in Asia (especially among the islands) distinct species arose, adapted to special food-plants and other conditions, and that whenever these spread so that their ranges overlapped, crossing—by throwing the organism out of gear with its environment—was injurious, and so tendencies to genitalic modification were preserved. If these arose by simultaneous mutation,[1] not by random scattering variation, they might in such a case lead to a pure differentiated race. Suggestions of this sort are of course to be taken with an adequate supply of salt, but they have their use as stimulating enquiry.

[1] Or, perhaps, were already present as Mendelian recessives?

Some years ago, in an address before the Entomological Society of London, Professor Poulton raised the question whether the ability to mate successfully was not after all something maintained by rigid natural selection; and if I remember his argument correctly (I do not possess a copy of his paper), he believed that differences in the sexual organs might be expected to arise whenever selection ceased to operate. Since that time Tower has produced striking evidence of the small amount of divergence which suffices to throw an organism (in his instances beetles) out of the race. In this connection it may also be remarked that the singular fertility between different races of men, dogs, cattle, etc.,—many of these differing exceedingly in many characters of color and form—may be attributed to the effects of natural selection. The purest breeds of dogs, and no doubt the best established races of men, are after all great mongrels; and in the course of time no doubt interracial infertility would be absolutely discriminated against. However active the imagination may be in picturing causes and effects, it can but pause before such cases of genitalic modification as are described by Dr. J. B. Smith in his revision of the moths of the genus Homoptera and its immediate allies, just published by the U. S. National Museum. In some of these moths the sexual organs are extremely asymmetrical. "In the males the asymmetry is between the harpes of the two sides, which in extreme cases are totally dissimilar, with processes on one side for which there is no counterpart on the other, and which are rarely entirely alike. The sheath of the penis or intromittent organ is always more or less curved or bent, or even hooked, and this structure is directly correlated to the differences found in the female." These peculiarities are all figured most carefully.

T. D. A. COCKERELL.

VERTEBRATE PALEONTOLOGY

The Lysorophidæ.—In 1875 Dr. J. C. Winslow, of Danville, Illinois, a local collector of fossils, discovered, at "Horseshoe Bend," on Salt Fork, on the Tate farm, some two miles south of Oakwood, in Vermilion County, Illinois, some bones which he sent to Professor Cope for identification. Later on the work of exploration at this place was taken up by Mr. W. F. E. Gurley and his collection was transferred to the University of

Chicago, where it now is. In 1877 Cope published a description of several forms from among the remains collected at "Horseshoe Bend" among which was the form *Lysorophus tricarinatus*, based on three vertebræ, which Cope took to be of reptilian nature. From the fact that the bones were very similar to some found in the Texas Permian, Cope concluded that the Illinois deposit was likewise Permian; and such it is usually regarded. From the discovery of a similar deposit in Pennsylvania by Raymond[1] it seems more probable that the deposit in Illinois is Pennsylvanian, as is the deposit in Pennsylvania.

In the summer of 1907 Dr. S. W. Williston sent the writer to the Illinois locality for the purpose of settling the stratigraphy, if possible, and to secure more material to illustrate the forms which are so meagerly known. The deposit was found to be already exhausted and after a month's work scarcely a handful of bones was secured. The stratigraphy was almost impossible of determination, though Dr. Stuart Weller, who visited the locality, was of the opinion that the circumstantial evidence was very strong in favor of its being upper Pennsylvanian. Since the discovery of similar deposits in Pennsylvania of undoubted Pennsylvanian age it seems no longer necessary to doubt the Carboniferous age of these Illinois deposits. In 1902 in "Contributions from Walker Museum, Vol. I, p. 45," Case announced the discovery of typical vertebræ of the *Lysorophus tricarinatus* type from the Permian of Texas. Last June Case[2] described the skull of the *Lysorophus tricarinatus* and came to the conclusion that the form was an amphibian. Later in the summer and almost simultaneously papers by Broili[3] and Williston[4] appeared on the same subject. Broili emphatically denied the amphibian nature of Lysorophus and Williston proved conclusively that the form is not only an amphibian, but is even allied to the modern Urodela. Broili reaches the most astonishing conclusion that Lysorophus "erscheint daher nach den in der Systematik geltenden Grundsätzen für richtiger. . . . zu den Lacertiliern zu stellen."

Williston shows very conclusively that the form is an undoubted amphibian and gives the following characters to support his views: skull pointed with no evidence of orbits, paired

[1] *Science*, N. S., Vol. XXVI, No. 676.
[2] *Bull. Amer. Mus. Nat. Hist.*, Vol. XXIV, p. 531.
[3] Broili, *Anat. Anz.*, Bd. XXXIII, No. 11/12.
[4] Williston, *Biol. Bull.*, Vol. XV, No. 5.

epiotics present, supraoccipital unpaired, condyle unossified, *branchial apparatus well developed,* vertebral column slender, limbs apparently absent, ribs long, somewhat curved and flat, neurocentral. Williston concludes:

"The only aberrant character to distinguish Lysorophus from the Urodela is the long and rather broad ribs, unknown among these modern animals or their possible ancestors, the Branchiosauria. It is, however, very evident that the earliest ancestors of both these groups must have long ribs, and their persistence in Lysorophus would be nothing remarkable."

But why need we conclude that the early ancestors of the Amphibia must have had long ribs? There is no geological evidence of such, and the oldest known branchiosaurian, *Micrerpeton caudatum* Moodie from the middle Pennsylvanian certainly possesses very short ribs. The animals associated in the Carboniferous with the Branchiosauria, as a rule, possess long ribs, but do we need to infer that the Branchiosauria and the Microsauria had the same ancestry?

In all the long stretch of geological time there has never existed a branchiosaurian nor a true urodele which had long ribs, and so far, aside from the frogs found in the Tertiary, these are the only true amphibians known in the fossil state. It is exceedingly incongruous to class the Microsauria and Branchiosauria in the same order Stegocephala. Their organization is totally different. To be sure, the long ribs in Lysorophus might have developed secondarily as Williston suggests, but why do we need to assume even this when among the modern Gymnophiona we find long ribs and every other character which is present in the Lysorophus? It is also possible that the Gymnophiona are true Caudata, in which case there would be no distinction and it may be that Lysorophus will be of great assistance in bridging over this gap between the Caudata and the Gymnophiona.

Certain it is that the form is a most interesting discovery and one of the most important in the phylogeny of the extinct Amphibia in many years. I quote herewith from a letter to Dr. Williston from Dr. Broom which the former was so kind as to send me during the course of our correspondence on the subject:

"The skull (of Lysorophus) is to my mind undoubtedly Urodele and singularly like that of Amphiuma which I believe to be the nearest living ally. I am convinced that it is not a Gymnophionid . . ."

Here are then three various points of view offered for study—one, of Broili, that the form is a lacertian; two, that of Williston and Broom, that the form is a member of the true Caudata; three, the suggestion offered here that the form may be one of the Gymnophiona. In further support of the view of the gymnophionid character of the form is the snake-like character assumed by *Lysorophus*. Case has noted that the vertebral column is usually coiled where there is any considerable portion of it preserved and Dr. Williston remarked to the writer of the same fact which he had observed in the field while in Texas the past summer. The palate structure of the *Lysorophus* is against the idea of the form being a member of the Gymnophiona, at least so far as we know the palate; further knowledge of this structure will undoubtedly solve the problem.

Further study of the form will also reveal other facts as to its anatomy and we are hoping to hear much from the recent collections of Drs. Williston and Case from the Texas Permian.

Stegocephala.—In an endeavor to reach some definite conclusions in regard to the correct classification of the extinct Amphibia, investigators all over the world are issuing contributions on various phases of the subject. One of the more recent advances is a study of the vertebræ of the Carboniferous forms by Hugo Schwarz,[1] of Griefswald, Germany. He has studied the exact characters of the vertebræ of forms from the coal mines of Linton, Ohio, of which there are specimens preserved in Berlin and in Griefswald, and also specimens from Nürschan bei Pilsen. The work was done under the advice of Dr. Otto Jaekel and the paper shows a strong bias of Jaekel's views.

The methods of study adopted by Schwarz are the same as those proposed by Jaekel five years ago. The specimen is removed from the soft coal, in which it is imbedded, by chemicals and by mechanical means and an impression is made of the mold by wax, plaster or guttapercha. While most of Jaekel's results show that the methods have some advantages, yet it is to be doubted if they are the best in all cases. The interpretation of the material is a puzzle at the best, and when the elements are disturbed it is often very difficult to form any idea of their nature. Jaekel experienced this especially in his discovery of the "perisquamosal" in Diceratosaurus, a structure which does not exist in other species of this genus and was probably due

[1] *Beiträge zur Paleon. und Geol., Oesterreich-ungarns*, Bl. XXI.

to breakage in the form which Jaekel studied. Schwarz has, on the other hand, obtained excellent results, and his descriptions of the vertebræ of the various forms will be of great service to the student even though his conclusions are not accepted.

A new family "Ophiderpetontidæ" is proposed to include the genera Ophiderpeton and Thyrsidium, the former of which was included in Lydekker's Dolichosomatidæ. The family characters are solely those exhibited by the ribs and vertebræ. Under the heading of Ophiderpeton the author rediscusses the question of the "Kammplatten" and dismisses the subject with the remark "dass sie nichts mit den Stegocephalen zu tun haben." Herein he has committed an error, for Fritsch has distinctly figured[2] a nearly complete specimen of *Ophiderpeton persuadens* Fr. with the "Kammplatten" in place near the cloacal region of the animal. The whole question of the "Kammplatten" has recently[3] been reviewed by the present writer. There is a great deal of uncertainty as to what the true nature of the "Kammplatten" really is. That they do occur in selachians as stated by Fritsch[4] does not at all imply that they may not also occur in Ophiderpeton, and they certainly do occur here if Fritsch has correctly interpreted his specimen.

Schwarz adopts the two suborders Aistopoda and Microsauria for the "Holospondylen Stegocephalen," but does not seem to understand the differences which exist between these two suborders, and especially is this true when he includes the Ptyoniidæ in the Microsauria, since Ptyonius and its allies are typical members of the group Aistopoda. There is really but little difference between the groups Aistopoda and the Microsauria structurally, and, as Schwarz suggests, they undoubtedly arose from the same stem much as did the lizards and snakes, but they are just as distinctly members of different groups as are the Lacertilia and Ophidia. No form is more typically an aistopod than the Ptyonius. The subordinal characters are found in the vertebræ, in the lack of limbs, the elongation of the body and especially in the attenuation of the skull with its concomitant structural differences.

The final conclusion attained by the author is that, with Jaekel, he would divide the Stegocephala into two groups, the

[2] Fritsch, 1901, "Fauna der Gaskohle," Supplement, Vol. IV, p. 89.
[3] *Biol. Bulletin*, Vol. XIV, No. 4, 1908.
[4] *Sitzungsberichte der Boh. Gesell.*, 1905.

temnospondylous groups and the holospondylous group. In the first group he would place all the forms which possess rhachitomous, embolomerous and stereospondylous vertebra, and in the second group the forms which are usually known as Aistopoda and Microsauria. He evidently excludes the Branchiosauria from the Stegocephala proper, in which the present writer heartily agrees.

The contribution is a distinct advance in the knowledge of the forms described and it is to be hoped that we may have more information on the European forms which have been only too little studied and described.

The Cotylosauria.—The anatomy of this peculiar group of reptiles has been further elucidated by the recent studies of Williston[1] and Broili.[2] Williston restudied the form first described by Cope under the name of *Parioticus incisirus*. The University of Chicago possesses a nearly complete skeleton of this form and from his studies of this specimen Williston reached the conclusion that the form belongs rather in the genus Labidosaurus and is a typical cotylosaurian. He has given detailed figures of the anatomy of the various portions of the skeleton and a restoration of the form in so far as it is known. Broili has also given a restoration of a species of Labidosaurus, *L. hamatus*. He has mounted the entire skeleton free. This was impossible in the case of the specimen studied by Williston. Broili's restoration is a welcome addition to the knowledge of the Cotylosauria, although I am sure the animal, were he alive, would prefer not to have such an awkward sway in his vertebral column. One of the peculiar things about the Cotylosauria is the absence of lateral line canals which might be expected to be present from the close resemblance in their organization to the Stereospondyli, in which these canals are well developed. Dr. Williston searched carefully for the canals, but without success. The presence or absence of the canals may, at some future time, be one of the chief distinguishing characters between the forms which we call reptilian and those we call amphibian.

As a postscript to his article on Lysorophus[3] Williston has figured and described the ventral ribs of *Labidosaurus incisirus*.

[1] *Journ. Geol.*, Vol. XVI, No. 2, 1908.
[2] *Zeit. Deutsch. geol. Gesell.*, Bd. 60, H. 1, 1908.
[3] *Biol. Bull.*, Vol. XV, No. 5, 1908.

From the presence of these small abdominal ribs Williston concludes that: "This character adds another evidence of the relationship between the Procolophonia and Labidosaurus, and destroys its value as a group distinction." Broili, on the other hand, sees closer relationship between the Cotylosauria and the Stegocephala.

The Oldest Known Reptile.[1]—Dr. S. W. Williston has recently redescribed the type specimen of the oldest known reptile. This form, which Williston proposes to call *Isodectes copei* sp. nov., was doubtfully referred by Cope to the genus Tuditanus, but subsequently he referred it to the Texas genus Isodectes. It certainly does not belong in Tuditanus, and while there is no positive evidence that the form belongs in the genus Isodectes it seems well to leave it there until the characters of Isodectes are better known. The specimen is No. 4457 of the U. S. National Museum. It is preserved in a block of soft coal from the Linton mines of Ohio which have furnished nearly all of the remains of Carboniferous quadrupeds yet known in North America. The Linton mines were undoubtedly located well down in the Pennsylvanian and there has not yet been described a reptile from a lower horizon. The affinities of the form are doubtful though its close relationship to the Microsauria is well established. The intercentral attachment of the ribs and the apparent loss of the hypocentra in *Isodectes copei*, may require a revision of the theory of the formation of the reptilian vertebrae. The absence of abdominal ribs in this form is significant in the light of the recent discussions of the relationships of the early reptiles.

The Age of the Gaskohle.—Students of vertebrates the world over have become accustomed to accepting Fritsch's interpretation of the age of the Gaskohle of Bohemia as Permian. It is with some surprise, though not a little gratification, to note that through the recent studies of European geologists and paleontologists the deposits in Bohemia are now being regarded as Upper Carboniferous. The facts and arguments are well set forth by Broili[1] in a recent discussion on Sclerocephalus. Besides thus adding to the stratification of the forms of Amphibia the new fact is thus brought out that the large form Sclero-

[1] *Journ. Geol.*, Vol. XVI, No. 5.

[1] *Jahrbuch d. K. K. Geol. Reichsan.*, Bd. LVIII, H. I.

cephalus, which is possibly temnospondylous, occurs first in the Upper Carboniferous. A close parallel of this is found in the discovery of *Eryops* by Case[2] in the Upper Pennsylvanian of Pennsylvania. The progress of discovery is thus forcing further and further back into geological time the origin of the Amphibia. We now know nearly all of the types of the so-called Stegocephala from the Carboniferous and some of them occur well down in the system.

The results given by Broili are based in large part on the geological and paleobotanical studies of Weithofer and Feistmantel. The report is a lengthy one and occupies some twenty pages, including lists of the vertebrates and the plants which occur in the "Gaskohle schichten."

Bison occidentalis.—In the last issue of the *Kansas University Science Bulletin* Dr. C. E. McClung[1] has described and figured a mounted skeleton of *Bison occidentalis*. This specimen was first noted by Williston in 1902.[2] It was later[3] described by Stewart as belonging to the species *B. antiquus* which is now assigned to *B. occidentalis*. The skeleton has only recently been mounted by Mr. H. T. Martin and is noteworthy as being the only mounted skeleton of a Pleistocene bison. The specimen is further noteworthy because of an arrow point found under the right scapula as if it had been imbedded in the flesh before death. From his study of the mounted skeleton Dr. McClung reaches the conclusion that the extinct species was of a more cursorial type than is the modern *Bison bison*.

Nectosaurus.—Three years ago Dr. J. C. Merriam[1] gave to the world a memoir on a peculiar group of marine reptiles which he had discovered in the Triassic rocks of California and to which he gave the appropriate name of Thalattosauria. He has recently[2] added to the knowledge of the Thalattosauria by additional notes on the anatomy of Nectosaurus. From his recent studies Merriam concludes that Nectosaurus is a shore dwelling form and the evidence seems strong enough to warrant

[2] *Annals Carnegie Museum*, Vol. IV, No. III–IV, 1908.
[1] *Kans. Univ. Sci. Bull.*, Vol. IV, No. 10.
[2] *Amer. Geol.*, Vol. XXX, International Congress of Americanists, 1902.
[3] *Kansas Univ. Quarterly*, 1897.
[1] *Memoirs Calif. Acad. Science*, Vol. V, No. 1.
[2] *University of California Publications, Geology*, Vol. 5, No. 13.

the conclusion that Nectosaurus is not a young form of Thalattosaurus as the author suspected when he wrote his memoir on the Thalattosauria.

Callibrachion.—F. von Huene has restudied[1] the original specimen of *Callibrachion gaudryi* Boule and Glan. from the figure published in *Mem. Soc. d'Hist. Nat. d'Autun*, 1893, Taf. 3, and has republished this figure as a page plate. He was led to this study by the fact that the three incongruous characters of coronoid process of the mandible, opisthocœlous cervicals and the presence of only about 20 presacral vertebræ being assigned to the form and on these characters it had been assigned to the Protorosauria by earlier authors and later to the Pelycosauria and here it is placed by Case in his "Revision of the Pelycosauria." Huene comes to the conclusion that the form is a close relative of Paleohatteria

"Hieraus folgt, dass Callibrachion nicht zu den Pelycosaurien gehören kann, sondern sich Paleohatteria sehr nahe anschliesst und wohl als einer ihrer direkten Nachkommen aufzufassen ist."

He is then of the opinion that the earlier authors were right in assigning Callibrachion to the Protorosauria. There are 23 presacral vertebræ whch are amphicœlous as in the Paleohatteria. The coronoid process is wanting in Callibrachion.

Roy L. Moodie.

PARASITOLOGY

The Sleeping Sickness Bureau, recently established in London, has begun the publication of a bulletin. The first number (October, 1908) is devoted to a review of the "Chemotherapy of Trypanosomiasis." The treatment of trypanosomiasis in man, the biological accommodation of trypanosomes to chemotherapeutic agents and the treatment of experimental animals are considered in succession. A bibliography of some 200 titles concludes the number. Future issues of the bulletin will include all the current literature of trypanosomiasis.

The following items excerpted from the summary of this mass of experimental material are of primary biologic interest. The use of any trypanocide by itself can not be justified. Combined therapy has the advantage that each drug can be used in smaller doses. The alternation of trypanocidal agents avoids the habituation of the parasites to a single remedy which has been thor-

[1] *Centralblatt für Mineral. Geol. Paleontologie*, 1908, No. 17.

oughly demonstrated through laboratory experiments. A second paper deals with the medical results of segregation camps and of chemical therapy in Uganda.

In the Huxley lecture, delivered at Charing Cross Hospital, October 1, 1908, Sir Patrick Manson, speaking on "Recent Advances in Science and their Bearing on Medicine and Surgery," discussed some points of great interest to biologists. At the start he noted the propriety of this theme for a Huxley lecture since the successful study of tropical diseases both depends on the use of those methods so consistently and powerfully employed by that great master of natural science, and also deals primarily with animal organisms, protozoa and helminthes, as disease producers and their special vectors, commonly arthropods, while bacteriology is relegated to a secondary place. In the study or teaching of tropical medicine this fact must be recognized by the addition to each staff of a protozoologist, a helminthologist, and an arthropodologist with suitable library and laboratory facilities. After presenting a synoptic table which outlines the principal tropical diseases with their causal and intermediary agents, the lecturer proceeds to discuss the appropriateness and value of biological theories in scientific advance with special reference to this field. Certain blood-inhabiting protozoa require a second host as a medium for a sexual cycle, as for instance the malarial plasmodium makes use of the mosquito. Is this to be regarded as a general law applicable to all such protozoa? The answer to this question is of fundamental importance in practical medicine as well as of intense interest to the biologist. The case of the sleeping sickness trypanosome will serve as an example for testing the problem.

The chief argument in favor of such a law is to be found in analogy, and though it must be used with caution the evidence in this case is distinctly favorable. All animals appear to require periodic sexual changes, and in other protozoa a sexual cycle necessarily interrupts the periods of asexual reproduction if the existence of the species is to be prolonged beyond narrow limits. In many cases where the existence of such a sexual cycle had long been denied it has been demonstrated by more intensive study. So highly developed a form as the trypanosome can hardly be an exception to this rule. By analogy such a stage would be found outside the human body and probably in the appropriate carrier of the disease, the tsetse fly.

On the other hand, four arguments have been brought forward against the acceptance of such a law: (1) No such sexual phase has yet been demonstrated in any trypanosome. The history of science gives scant weight to such negative evidence, especially when one considers the minuteness of the organism and the refractory character of the object studied, the tsetse fly. (2) The sexual phase of the trypanosome may be passed in the vertebrate blood and thus the tsetse fly be a mere mechanical carrier. There is, however, no evidence favorable to this view, either in observation or by analogy. (3) The successful inoculation of the trypanosomes through a long series of vertebrate hosts has been held to indicate that a sexual cycle is unnecessary. Yet similar laboratory transfer has been practised with the malarial plasmodium, for instance, though such a sexual cycle in the mosquito is demonstrated beyond all question. (4) An insect intermediary is apparently unnecessary in one trypanosome, that which causes dourine or mal du coit in horses, and therefore is not a biological necessity in any other species of trypanosome. This Sir Patrick Manson regards as the most formidable argument yet advanced against the law under discussion, but does not consider it as final. He devotes much space to the consideration of details in the case and the presentation of an alternative hypothesis which is too involved to reproduce in abstract. While the discussion presents many points of interest, yet the entire absence of experimental evidence in its support leaves this view as at present a bare working hypothesis. It may be added further that even the total rejection of this hypothesis does not necessitate the adaption of the view it combats. Much further investigation is needed before one can say with any confidence how the evidently exceptional case of the dourine trypanosome is to be explained. He concludes:

"I hold, therefore, that the existence of a sexual phase in the sleeping-sickness trypanosome, *T. gambiense*, and other trypanosomes, is more than probable, and that it has not been disproved; that the argument founded on the natural direct communicability of dourine in the apparent absence of an insect intermediary for its germ, *T. equiperdum*, is not valid; and that the evidence hitherto adduced is distinctly in favor of a law to the effect that blood-haunting protozoa having arthropod vectors require, and make use of, these vectors for necessary sexual development. Why the sexual stage of these parasites is passed in the arthropod, and not in the vertebrate, I cannot explain,

any more than I can explain the contrary arrangement which obtains in the blood-haunting nematodes, the sexual stage in their case being passed in the vertebrate host, the asexual in the insect.

"I have no doubt, while listening to these remarks, it has occurred to some of you, as it has often occurred to me, that the principles I have endeavored to express have a wider application than that which I have directly indicated, that our disease germs and our ectozoa—insignificant though the latter appear to be—are correlated more frequently than is generally suspected; that, in fact, there is a necessary relationship between them." HENRY B. WARD.

EXPLORATION

Camp-fires on Desert and Lava.[1]—Lovers of outdoor life in the far distant west will be delighted on opening W. T. Hornaday's recent work, "Camp-fires on Desert and Lava," to observe, on the back of the half title page, a figure of the omnipresent Eleodes in very characteristic attitude. This little black creature by his position seems to be pointing us heavenward, but far from it. He is ever ready to present us with a drop of sticky brown fluid which has a horrible odor and whose stain will withstand the strongest soaps. The beetle forms a fitting introduction to the delightful account which follows.

The author needs no introduction to the reading public nor to the zoologist. To the one he is already well known by his previous volumes and to the other by his connection with the National Museum and with the New York Zoological Park as well as by his scientific writings, not the least important of which is his "Extermination of the American Bison," published in 1889. Mr. Hornaday is an enthusiastic collector and observer. All those who follow him into the Pinacate region, described in the present work, will never regret it.

On our present maps the region visited by Mr. Hornaday and his friends is variously located; suffice it to say that it is in the northwestern part of Mexico and not many miles from the Gulf of California. The region was attractive for several reasons, among which was the one that it had never been explored by any scientist or if it had there was no record of it. Other reasons which attracted the party to the region were the possible presence of big game and for Dr. MacDougal, who originated the plan, there were untold new plants, of a type very interesting to him, to be discovered. Dr. D. T. MacDougal made

[1] William T. Hornaday, Camp-fires on Desert and Lava. Illustrated. Charles Scribner's Sons, New York, 1908.

up the expedition under the auspices of the Carnegie Institution to extend his researches on the desert flora, and on the journey down to Mexico the author tells us of their visit to the famous "Desert Botanical Garden" near Tucson, Arizona, of which Dr. MacDougal was one of the originators, and from which point the expedition outfitted.

To those who have explored in the semi-arid regions of the western states the account given by Mr. Hornaday of their cross-country trip, recalls many familiar scenes. The cold mornings, the blistering hot days and the delightfully cool evenings are all features of a trip into the desert regions of the west. All the scenes along the trail are brought before the reader by pictures from pen and camera. The colored photographs are especially striking. Botanists will find an interesting account of the desert flora of southern Arizona and northern Mexico and the zoologist will find a description of the few animals which can manage to exist in this forlorn region. There is ever an attraction in the desert; even the barrenness of things and the apparent absence of all life make what little life there is all the more interesting.

On the arrival of the party near the Pinacate region a long camp was made and short exploring trips were conducted from the main camp. This was made necessary from the fact that the character of the country forbade further progress with the wagons. At this place also occurred the only "row" of the trip. Old campers know how painful it is to have a "row" on in camp. It is painful for those immediately concerned and for those who have to witness it. Their stay at Pinacate was of some length and full of success. They secured much big game and saw many interesting plants and photographed many new plants and craters which abounded there. The most abundant large mammal was the mountain sheep, *Ovis canadensis*. The author gives, in chapter XXIV, a discussion of the geographical distribution of the mountain sheep and also the synonymy of the species and subspecies of this interesting group of ungulates.

The last two chapters tell of the flight from Pinacate and the return to civilization. "The reaction from the steady and severe rush of the trip left us limp and spiritless, and it was four full days ere one member of the party began to feel quite like himself again." Thus ends the account of this unique exploring trip into the unknown regions of the southwest.

ROY L. MOODIE.

The American Naturalist

A Monthly Journal, established in 1867, Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Organic Evolution and Heredity

CONTENTS OF THE AUGUST NUMBER

The Mid-summer Bird Life of Illinois: A Statistical Study. Professor S. A. FORBES.

The Life Cycle of Paramecium when subjected to a Varied Environment. DR. LORANDE LOSS WOODRUFF.

Placobdella Pediculata n. sp. ERNEST E. HEMINWAY.

Marine Laboratories and our Atlantic Coast. DR. ALFRED G. MAYER.

Biometry as a Method in Taxonomy. Professor CHARLES LINCOLN EDWARDS.

Shorter Articles and Correspondence: The Genus Ptilocrinus, AUSTIN HOBART CLARK. A New Rhinoceros from the Lower Miocene of Nebraska, HAROLD JAMES COOK.

Notes and Literature: *Plant Cytology*—Some Recent Research on the Cilia-forming Organ of Plant Cells, DR. BRADLEY M. DAVIS. *Ornithology*—Riddle on the Genesis of Fault-bars and the Cause of Alternation of Light and Dark Bars in Feathers, J. A. A. *Herpetology*—Ruthven's Variations and Genetic Relationships of the Garter-snakes, J. A. A. *Lepidoptera*—Hybrid Lepidoptera, Professor T. D. A. COCKERELL.

CONTENTS OF SEPTEMBER NUMBER

Some results of the Florissant Expedition of 1908. Professor T. D. A. COCKERELL.

Embryology of Myosurus Minimus. DR. LEROY D. SWINGLE.

Another Aspect of the Species Question. DR. J. A. ALLEN.

The Origin of the Lateral Eyes of Vertebrates Professor G. H. PARKER.

Notes and Literature: *Heredity*—Spurious Allelomorphism, Results of Some Recent Investigations, W. J. SPILLMAN. *Human Anatomy*—Pryor on Sexual and Family Variation in Centers of Ossification, C. R. B *Plant Cytology*—Cytological Studies on Saprolegnia and Vaucheria. DR. BRADLEY M. DAVIS. *Holothurians*—Holothurioidea, Professor CHARLES L. EDWARDS. *Enteropneusta*—Recent Literature on the Enteropneusta, Professor W. E. RITTER. *Vertebrate Paleontology*—Case on Pelycosauria of North America; Barnum Brown on the Conrad Fissure and on the Ankylosauridæ. Professor S. W. WILLISTON. *Parasitology*—The Evolution of Parasitism; Trypanosomes, H. B. W.

CONTENTS OF THE OCTOBER NUMBER

The Manifestations of the Principles of Chemical Mechanics in the Living Plant. DR. F. F. BLACKMAN.

The Desiccation of Rotifers. D. D. WHITNEY.

On the Habits and the Pose of the Sauropodous Dinosaurs, especially of Diplodocus. DR. OLIVER P. HAY.

Shorter Articles and Correspondence: Juvenile Substitutes for Smoking Tobacco. Professor WILLIAM ALBERT SETCHELL.

Notes and Literature: *Heredity*—Recent Studies in Human Heredity, DR. F. A. WOODS. *Ornithology*—Riddle on the Cause of the Production of Down and Down-like Structures in the Plumages of Birds, J. A. A. *Vertebrate Paleontology*—New Fossil Mammals from Egypt, T. D. A. C.

CONTENTS OF THE NOVEMBER NUMBER

Further Studies on the Activities of Araneads. Professor THOS. H. MONTGOMERY, JR.

Notes on the Daily Life and Food of Cambarus Bartonius Bartoni. FLOYD E. CHIDESTER.

Some Points in the Ecology of Recent Crinoids. AUSTIN HOBART CLARK.

Shorter Articles and Correspondence: Evolution without Isolation, O. F. COOK. A Note on the Silverside, JOHN TREADWELL NICHOLS.

Notes and Literature: *Botany*—The Origin of a Land Flora, Professor DOUGLASS HOUGHTON CAMPBELL. *Plant Cytology*—Apogamy in the Ferns, DR. BRADLEY M. DAVIS. *Experimental Evolution*—Regeneration in Lumbriculus, SERGIUS MORGULIS. *The Budgett Memorial Volume*—John Samuel Budgett, President DAVID STARR JORDAN. *Animal Behavior*—Mind in Animals, Professor H. S. JENNINGS.

CONTENTS OF THE DECEMBER NUMBER

Some Physiological Aspects of Radium Rays. Professor C. STUART GAGER.

On the Origin of Structures in Plants. W. A. CANNON.

Origin and Formation of the Froth in Spittle Insects. BRAXTON H. GUILBEAU.

Shorter Articles and Correspondence: Peculiar Abnormal Teeth in a Jack Rabbit. WILLIAM A. HILTON.

Notes and Literature: *Ichthyology*—Ichthyological Notes, President DAVID STARR JORDAN. *The Inheritance of Sex in Higher Plants*—Digest of Professor C. Correns's Memoir: Professor H. E. JORDAN.

Title Page and Index to Volume XLII.

CONTENTS OF THE JANUARY NUMBER

Juvenile Kelps and the Recapitulation Theory. Professor ROBERT F. GRIGGS.

The Larva and Spat of the Canadian Oyster, DR. J. STAFFORD.

Shorter Articles and Correspondence: Some Notes on the Traditions of the Natives of Northeastern Siberia about the Mammoth, WALDEMAR JOCHELSON. Age of Trotting Horse Sires, F. R. MARSHALL. The Occurrence of *Batrachoceps attenuatus* and *Autodax lugubris* in Southern California, WILLIAM A. HILTON.

Notes and Literature: *Experimental Evolution*—The Effect of the Environment upon Animals, DR. FRANK E. LUTZ. *Experimental Zoology*—The Influence of the Size of the Egg and Temperature on the Growth of the Frog, SERGIUS MORGULIS. *Parasitology*—Cestodes of Birds, Professor HENRY B. WARD.

Single Number 35 Cents **Yearly Subscription, $4.00**

The NATURALIST will be sent to new subscribers for four months for One Dollar

THE SCIENCE PRESS

Garrison, N. Y. **Sub-Station 84: NEW YORK** **Lancaster, Pa.**

Animal Micrology

Practical Exercises in Microscopical Methods

By

MICHAEL F. GUYER

---

250 pages, 8vo, cloth; net $1.75, postpaid $1.88

THE title of this book will explain its scope. It is intended as a laboratory manual for textbook use. Its aim is to introduce the student to the technique of microscopic anatomy and embryology, emphasizing details of procedure rather than descriptions of reagents or apparatus. Sufficient account of the theoretical side of microscopy is given to enable the student to get satisfactory results from his microscope.

The directions are simple, explicit, and complete.—*American Journal of Clinical Medicine.*

The medical student will find it very useful as a guide to microscopic work.—*Journal of the American Medical Association.*

This is one of the cleanest works on microscopical technique we have ever seen, and is especially suitable for the beginner. It is full of points, tricks of technique not mentioned in other works, and is one that every student and physician should have.—*Medical Century.*

This valuable book is strong through its rigid exclusion of the trite and the conflicting. It is lucid and helpful, because a man long practiced in practical work has given what he believes the most expeditious and reliable method of obtaining a definite and comprehensive result.—*Medical Notes and Queries.*

A concise, eminently practical, and well-classified treatment.—*Science.*

The expositions of the methods recommended are admirably clear.—*Nature.*

One of the best and most practical works upon microscopic technique with which we are acquainted.—*American Naturalist.*

As a textbook it can hardly be improved. The research worker will find in this book just the information he frequently needs in preparing material with which he is not familiar.—*School Review.*

It does present in very clear form a judicious selection of methods, including an excellent untechnical account of the microscope and its optical principles, adequate for the undergraduate course in histology.—*Journal of Comparative Neurology and Psychology.*

Address Dept. 62

The University of Chicago Press

CHICAGO NEW YORK

VOL. XLIII, NO. 507 MARCH, 1909

THE AMERICAN NATURALIST

A MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

CONTENTS

		Page
I.	Invitation Papers at the Baltimore Meeting of the Botanical Society of America; Darwin Memorial Session:—	
	Darwin as a Naturalist; Darwin's Work on Cross Pollination in Plants. Professor WILLIAM TRELEASE	131
	Darwin's Influence upon Plant Geography and Ecology. Professor FREDERIC E. CLEMENTS.	143
	Darwin's Work on Movement in Plants. Professor HERBERT MAULE RICHARDS.	152
II.	An Examination of Darwin's "Origin of Species" in the Light of Recent Observations and Experiments. Professor EDWIN LINTON.	163
III.	The Distinction between Development and Heredity in Inbreeding. Dr. EDWARD M. EAST.	173
IV.	Breeding Experiments with Rats. Professor T. H. MORGAN.	182
V.	Shorter Articles and Discussion: The Chub and the Texas Horn Fly, DR. ROY L. MOODIE. A New Camel from the Lower Miocene of Nebraska, HAROLD JAMES COOK	186
VI.	Notes and Literature: *Heredity*—The Chondriosomes as Bearers of the Hereditary Qualities, F. PAYNE. Cultural Bed Mutations in the Potato.	190

THE SCIENCE PRESS

LANCASTER, PA. GARRISON, N. Y.

NEW YORK: SUB-STATION 84

The American Naturalist

MSS. intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS

Lancaster, Pa. Garrison, N. Y.

NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

Important New Scientific Books

PUBLISHED BY THE MACMILLAN COMPNY

Botany

The Origin of a Land Flora. A Theory based upon the facts of Alternation. By F. O. Bower, Sc.D., F.R.S. With numerous illustrations.

Cloth, gilt top, xi+727 pp., illus., index, 8vo, $5.50 net.

Note.—A profound study in the morphology of the lowest forms of plants, with special reference to the development of their reproductive systems. The author endeavors to show that the present land flora has originated from an aquatic ancestor, and traces the methods of specialization to the land habit, and the establishment of the forms of the higher plants. A book of the highest importance not only to botanists but to biologists in general.

NEW AND STANDARD HAND-BOOKS ON AGRICULTURE, ETC.

Elements of Agriculture, Southern and Western. By W. C. Welborn, B.S., M.S., M.P.A.

Cloth, xvi+329 pp., illus., appendix, glossary, index, 12mo, $.75 net.

Note.—This is a thoroughly modern treatise on farming as practiced in the Gulf States, rrom the point of view of the scientific agriculturist. It is adapted to school use, but is of practical service to any farmer in that part of the country. The author is vice-director of the Texas Experiment Station.

Re-issues of the highly valued Hand-Books known as the Garden Craft and Rural Science Series, edited by L. H. BAILEY, of Cornell University, Editor of "Cyclopedia of American Horticulture," "Cyclopedia of American Agriculture," etc.

The Principles of Fruit Growing. By L. H. Bailey.
Tenth Edition, $1.50 net, by mail $1.66.

Irrigation and Drainage. By F. H. King.
Fifth Edition, $1.50 net, by mail $1.68.

Principles of Vegetable Gardening. By L. H. Bailey.
Sixth Edition, $1.50 net, by mail $1.68.

Bush Fruits. By Fred W. Card.
Fourth Edition, $1.50 net, by mail $1.66.

Fertilizers. By Edward B. Voorhees.
Tenth Edition, $1.25 net, by mail $1.38

Farm Poultry. By Geo. C. Watson.
Sixth Edition, $1.25 net, by mail $1.42

Published By **The Macmillan Company** 64-66 5th Ave., New York

THE
AMERICAN NATURALIST

VOL. XLIII *March, 1909* No. 507

INVITATION PAPERS AT THE BALTIMORE MEETING OF THE BOTANICAL SOCIETY OF AMERICA

AT the recent Baltimore meeting of the Botanical Society of America, three series of special papers were read by members who were specially requested by the council of the society to prepare them for the occasion.

The first set of papers dealt with certain phases of recent advance in our knowledge of vascular anatomy in plants. These papers, read on December 29, were by J. M. Coulter and E. C. Jeffrey.

The papers of the second series were read at a symposium on "Present Problems in Plant Ecology," on Wednesday, December 30. The participants were H. C. Cowles, B. E. Livingston, C. H. Shaw, V. M. Spalding and E. N. Transeau.

The papers of the third series were read at the Darwin Memorial Session, held on Thursday, December, 31. These addresses gave estimates of Darwin's work in three fields of botanical investigation. The participants were Wm. Trelease, F. E. Clements and H. M. Richards.

In accordance with the instructions of the society, all of the above mentioned papers are here published in full.

DUNCAN S. JOHNSON,
Secretary.

OFFICE OF THE SECRETARY,
BALTIMORE, MD., February 1, 1909.

DARWIN MEMORIAL SESSION

In response to a letter announcing the plans for the Darwin Memorial Session, and suggesting that some

word of greeting on that occasion would be very appropriate, and pleasing to his botanical colleagues in America, Professor Francis Darwin sent the following letter to the president of the Botanical Society of America. It arrived, unfortunately, for a reason stated in the letter, too late for the meeting, but it obviously belongs with the other contributions thereto.

13, Madingley Road, Cambridge. Dec. 23, '08.

Dear Sir;

Owing to absence from home I am only now able to answer your very kind letter. I am afraid my answer can not reach you in time, which I much regret. I should have liked to express thro'h you as president my sympathy with this assembling of American botanists to honour my father's memory. It is a source of sincere satisfaction to me to know that such a meeting is to be held. I am reminded of my father's words to Asa Gray:

"Hooker has forwarded to me your letter to him; and I can not express how deeply it has gratified me. To receive the approval of a man whom one has long sincerely respected, and whose judgment and knowledge are most universally admitted, is the highest reward an author can possibly wish for."

Your meeting is a posthumous "reward," and though I have no right to speak for English botanists I know that they will appreciate it as it deserves.

Yours sincerely,

Francis Darwin.

DARWIN AS A NATURALIST: DARWIN'S WORK ON CROSS POLLINATION IN PLANTS

PROFESSOR WILLIAM TRELEASE

WASHINGTON UNIVERSITY

CHARLES DARWIN is rated as a great man, and there are really not many to-day who would dispute his title to this verdict; but he did not come easily to it.

In botany, he never did a thesis on morphology or cytology, or photosynthesis; he was puzzled rather than deranged by nomenclature; the reason that he provided for the compilation of an index to the names and authorities of all known flowering plants and their countries, in a way, is a confession that he was not a taxonomist; and a really fair all-round doctor's examination, with botany as a major, would have been likely to give him more than the proverbial trouble. He does not seem to have considered himself a botanist, and perhaps has never been admitted to the fraternity formally—though he has opened our eyes to some of the most interesting aspects of plant physiology, baring their secrets in a masterly way with the rough-and-ready direct methods and apparatus of an adept.

His earlier publications were on geology and zoology. My impression is that botanists—aside from the very few who know—looked on him in his lifetime rather as a zoologist. And yet even to-day amusement may be derived from reading what has been made public of the debate before the French Academy, when his name was under discussion for membership in the zoological section of that great body and one of the immortals was ready to place a hundred zoologists before him because of their contributions of demonstrable facts to the science.

The greatness of the man itself long stood in the way of its recognition. He had not classed himself with suffi-

cient minuteness in the subdivision of science. Looking back on his career, it is not difficult to see that the geological problems opened up to him by the voyage of the "Beagle" would have afforded an interesting field for detailed life work in geology which would have placed him quickly among the foremost geologists of his day if he had devoted himself to them and continued to publish on that subject and for those specialists. Even the French savants saw in his barnacle studies the work of far more than a tyro; but he did not choose to devote himself to the morphology and classification of animals. So little had he been thought of generally as knowing anything of botany, that the *Gardeners' Chronicle* reviewer of his orchid book expressed himself as doubly constrained to care in critically analyzing it. He was somewhat like a versatile witness questioned individually by the members of a polyglot jury, each using and understanding his own language and getting nothing more than a minute fragment of the whole testimony: he can hardly be said to have had a hearing before his peers—of whom it would have been hard, even, to draw a full panel at any time in the world's history.

Darwin was really a philosopher. His son speaks of him as seeming to be so charged with a theorizing power that no fact, however small, could avoid releasing a stream of theory which itself magnified the fact in importance; but just enough to his theories not to condemn them unheard, so that he was willing to test what would seem to most people not at all worth testing. This is at once the key note to his life work and his greatness in influencing human thought. Though his philosophy has received unusual, and perhaps undue, attention, through clashing with some of what had become incorporated in the theology of his day, his service in molding our way of seeing nature may be coordinated with that of the great men who have reduced the movements of the planets to a physical basis and the transmutations of matter to terms of chemistry.

Curiously, the human mind of the twentieth century does not seem to be superior as a reasoning machine to that of the time of the Greeks, and it is not surprising that the general conclusions of Darwin's philosophy had been reached in one form or another all the way along the past three thousand years. That his name goes into history as their father, results from the way in which he arrived at and substantiated them rather than from their novelty: his greatness in great thought is the natural achievement of a large mind reaching its ends by way of the painstaking study of little things.

So full a discussion of Darwin from many points of view is provided in the symposium of our fellow society, the American Association for the Advancement of Science, and in the allotment of subjects for our own Darwin-session, that I should use time to little advantage if I were to go into illustration of this, outside the special field assigned me on the program—to the discussion of which I have been asked to preface this general introduction.

I wish that I might quote Darwin's first utterance on the subject that has been assigned specially to me for this meeting, but I do not know where to find it. In his autobiography, he states that in 1838 or 1839 he had begun to attend to the cross fertilization of flowers by means of insects, from having come to the conclusion in his speculations on the origin of species, that crossing played an important part in keeping specific forms constant. Even then he had noticed the floral dimorphism of *Linum*. In the preface to his book on the fertilization of orchids he explains that its publication resulted from the criticized exclusion (because of lack of space) of detailed facts substantiating an opinion expressed in his work on the origin of species, that it is apparently a universal law of nature that no hermaphrodite fertilizes itself for a perpetuity of generations—a law which he has stated in a variety of other phrases, and the suggestion of which he owed to Knight. The introductory

chapter of his book on the effects of cross and self-fertilization in the vegetable kingdom indicates that this conclusion, based on his personal observations on plants, was guided to a certain extent by the experience of breeders of animals (which is detailed at length in his book on the variation of animals and plants under domestication).

It was, therefore, not a novice who entered the botanical field when, in October, 1857, Darwin contributed a one-column note to the *Gardiners' Chronicle* on bees and fertilization of kidney beans, which he was attracted to through "believing that the brush on the pistil, its backward and forward curling movement, its protrusion on the left side, and the constant alighting of the bees on the same side, were not accidental coincidences, but were connected with, perhaps necessary to, the fertilisation of the flower." His subsequent papers and books, vivifying floral ecology, were therefore as inevitable from one who was moved by a new teleology in natural science as was the superb publication of a half century earlier by Sprengel, who, seeing the petal-hairs of a Geranium, sought after their meaning in the firm conviction that the wise Author of nature had not created even a hair in vain.

Darwin's publications in this field are not numerous; omitting abstracts and reprints of papers published in full, and later editions and translations, they number only twenty-two.[1] They are remarkably direct in purpose, simple in treatment, clear in reasoning, and free from a controversial or dictatorial spirit. His own observations and experiments were rarely accepted at their face value, but were checked up with rather unusual care; and, as we now know from his published letters, his conclusions were commonly subjected to the criticism of a very select private audience before going to the world at large.

The comprehensiveness of the studies underlying these publications may be indicated by the statement that

[1] See bibliography at end.

nearly 350 genera of plants, represented by about 600 species (several of them in a number of contrasted forms and varieties), are made the subject of comment. No insignificant proportion of this large number were under observation or experimental cultivation through a considerable number of years—the series on which the "Cross and Self-Fertilization" volume was based having been grown in numbers and with painstaking care through more than a decade; and the plants measured and the seeds counted were very many. No observer was so insignificant that his observations escaped analysis if they came to the knowledge of the great naturalist, though Darwin was sorely tried by the positive statement of some non-existent facts; and some of the prettiest workings of his mind are shown in the elimination of untenable conclusions which had been drawn by predecessors whose observations were recorded in sufficient detail to permit another to winnow them afresh. Enthusiasm in fitting his own observations into his theories occasionally led to error when facts were scanty or incompletely made out, but in such cases these were usually employed with a word of caution and errors were eliminated with a charming candor when discovered subsequently; and few writers have more gracefully accepted rectifications by others—even when bluntly phrased or embodied in aggressive criticism, as was sometimes the case.

First, last and always, his studies were directed to the species question, but in his pollination studies, as in every other field that he entered, he bent himself to collateral details with the zeal of a specialist. He was never oblivious to the treacherous frailty of small numbers and few series; but his innate soundness of judgment was checked and confirmed, here and there, through the rehandling of his data by one to whom the analysis of figures was a specialty. The dainty instruments of precision in the use of which physiologists train their undergraduate students, were neither used nor desired by him;

but his experiments were devised with very unusual expertness and, like his figures, made to reveal their own defects and reenforce one another as indicating directions of high probability even where they were seen to stop far short of proof.

The problems which Darwin here set before himself for solution were primarily the explanation of natural phenomena—most of which others had observed in a general way—which in his belief could not be meaningless. Though doubtless not his first essay, his first publication on the subject, in 1857, primarily stated observed facts in *Phaseolus* and attacked them in this spirit, but incidentally he analyzed the reasons why and how bees visit flowers and what their intelligence is, and faced the broad question why varieties of beans do not freely mix if their flowers are really so formed as to secure frequent intercrossing. The behavior of introduced plants separated from their natural pollinators, further came into the next paper, with a distinct enunciation of Knight's law. Why Vincas do not seed; what their pollinators are; the details and meaning of what Dr. Gray has called heterogony, understanding which gave him unparalleled satisfaction; why flowers of two or even three nominal genera should sometimes appear on one plant of *Catasetum;* the substantiation of Knight's law by detailed arguments of adaptation selected from a single family of plants; the reason why *Lythrum salicaria* is represented by three sets of individuals as distinct from each other in floral characters as if they belonged to different species, and incidentally why *Lagerstræmia* should possess a (less clearly analyzed) stamen-variability; why the wild oxlip should be held for a hybrid between other closely related primroses and why these are specifically distinct; an extensive experimental testing of the utility underlying Knight's law; and a comparative analysis of heterogony, sex-separation, and cleistogamy: these were the questions set for answer in subsequent publications.

The methods by which the problems were attacked were neither many nor complicated. Patience and forethought and perseverance are their chief characteristics. Observation, not exclusive of any discernible fact; experimentation, with control of the incidental results of manipulation; testing the parent condition of seeds supposed to be pure; consideration of alternative explanations of phenomena, and especially of those opposed to the conclusions adopted; counting, weighing, measuring —almost beyond belief; ingenious substitutions for insects in laboratory and garden observations on structures concerned in pollination; watching insects at work on flowers and supplementing such observation by notation of the record of their visits afforded by the flowers themselves; confirming the identity of doubtful pollinia on a moth by restoring their original color through moistening them; field observations at all hours and under all climatic conditions; ascertaining pollen-tube development in prepotency questions; painstaking pollinations to cover numerous permutations: such were the methods.

The results of Darwin's work in this field are not easily epitomized. It is not going too far to say that he secured universal recognition of Sprengel's unheeded demonstration that the structure of many flowers serves to ensure their pollination by unconscious insect aid; he broadened this by enough detail to warrant the conclusion that in general it serves to ensure cross-pollination by such aid, in this way substantiating Knight's law "nature intended that a sexual intercourse should take place between neighboring plants of the same species"; he gave experimental demonstration of the benefits of crossing, not in itself, but through the interbreeding of individuals which for several generations have been subjected to slightly different conditions, or as he puts it, to "what we call in our ignorance spontaneous variation"; and he showed at once the utility of assured partial self-fertilization as

effected by cleistogamic degradation, the benefits of assured crossing resulting from the combined structural and physiological differentiation characteristic of heterogony, and the probability that complete sex-separation "did not commence and was not completed for the sake of the advantages to be gained from cross-fertilization" —but has rather to do with the general problem of division of labor.

His manner of presenting conclusions is at once interesting, convincing and charming. Egotism abounds in his writings; but the "I" and the "my" are not those of the man thinking in first-person pronouns, but of one unwilling to speak in a cathedratic manner and careful to state even obvious conclusions as merely the results to which he as an individual had been unavoidably led. He wrestled with thought synonymy even more earnestly than men now do with that of species; and, for instance, by his use of the word "fertilization," not infrequently compels the reader to take his perfectly unescapable meaning broadly and not too literally; and his inability to find better words to express the significance of floral structures than "adaptation" and "contrivance," reveals the deep basic idea of teleologic causation that the human mind has embodied in the machinery for uttering human thought. His phraseology is often aphoristic. For instance: "No one will understand the final cause of the structure of many flowers without attending to this point" [resultant crossing]; "Who would have been bold enough to surmise that the propagation of a species should have depended on so complex, so apparently artificial, and yet so admirable an arrangement?" [as that in Catasetum]; "A fortunate accident for the plants" [if the detention of moths in securing *Orchis* nectar, long enough for the pollinia to harden on to them, were accidental]; "Nature abhors perpetual self-fertilization"; "Belief that flowers of any plant are habitually fertilized in the bud, or are perpetually self-fertilized, is a most

effective bar to really understanding their structure''; sexual differences may "characterize and keep separate the coexisting individuals of the same species in the same manner as they characterize and have kept separate those groups of individuals, produced from common parents during the lapse of ages or in different regions, which we rank and denominate as distinct species''; "Illegitimate unions [in heterogonous plants] are hybrids formed within the limits of one and the same species.''

Through it all, too, runs a thread of similar sentences revealing the soul of the man, groping only after the truth, to whom "the whole subject is as yet hidden in darkness.'' In this spirit he lived, worked and wrote. Quite apart from success in accomplishing the direct purpose for which he worked, he succeeded to an exceptional degree in stimulating the research instinct in others, and directing it into attractive and prolific fields, seeing realized almost immediately his prediction that what had been held for trivialities might, when understood, "exalt the whole vegetable kingdom in most persons' estimation.''

Things did not always go in his work as they were expected to—his first belief that if every bee in Britain were destroyed there would be no more pods on the kidney beans in that country, gave place to the certainty that a small percentage of fruit may set without such aid, and this particular species afterwards gave him less than the customary evidence of the benefits of crossing; but in general his expectation was sustained, or gave place to a better result for his general needs, and incidentally provided a wealth of detail consonant with his evolutionary theories and not yet known to be explicable on other grounds. Aside from this participation in his broader achievements, his work on floral ecology and fertilization, as has been said, has furnished one of the greatest stimuli of modern times to purposeful coordinated observation of minutiæ, not one of which is meaningless—in a field open to all who can see, whether or

not enjoying the privileges of great libraries and laboratories.

That he hovered very close to the edge of discoveries that were reserved for others, is clear to every one familiar with his publications. The effect of foreign pollen in modifying the seed (aside from the embryo) and fruit, was early known to him; but neither his studies nor those of others in his day were equal to the demonstration of double fertilization—even as to-day we go no further than the endosperm in accounting for these phenomena. Even his second botanical paper (1858) detailed at length a gardener's observations and his own experiments on a mongrel lot of beans which Darwin had the acuteness to test by growing some of the parent seed as well, and thus to demonstrate that this itself must have been crossed and not pure. Mendel's law—hardly deducible from these facts, but again suggested in his study of the heredity of style- and stamen-length in illegitimate unions of heterogonous species (which he contrasts with hybridization)—escaped him, and the obscurity of its publication seems to have prevented him from enjoying its benefits at all in his analysis of the complex problems of heredity. He was on the verge of knowing the important part that light sometimes plays in the phenomena of germination, but at most barely knew it. To him had not come the fundamental distinction between fluctuating and mutating variations; and the demonstration that cumulation of the latter and not accretion of the former underlies organic evolution was left for others—to whom the basal mystery of causation is likely long to remain as obscure as it confessedly was to Darwin. Convinced, beyond the possibility of doubt, of the benefits of sexual differentiation with attendant union of elements derived from different individuals, he paused before the question why this differentiation is beneficial up to a certain point and injurious if carried still farther; confessing in candor that he did not know what is the nature or degree of the differentiation, and

adding with characteristic humility that at the end he still stood in awe before the mystery of life.

Large as is his service to botany, even in the partial field assigned me on this program, it is but an incident in his life-long struggle with this great mystery on the border-line between the discoverable and the eternally unknowable.

Darwin's Publications on Pollination and Fertilization

1. Bees and fertilisation of kidney beans. Gard. Chron. **1857**: 725.
2. On the agency of bees in the fertilisation of papilionaceous flowers, and on the crossing of kidney beans. Gard. Chron. **1858**: 828–9.—Ann. & Mag. of Nat. Hist. iii. **2**: 459–465.
3. The origin of species by means of natural selection: or the preservation of favored races in the struggle for life. London, 1859, etc. Index.
4. Fertilisation of British orchids by insect agency. Gard. Chron. **1860**: 528.—Entomol. Weekly Intelligencer. **1860**.
5. Fertilisation of Vincas. Gard. Chron. **1861**: 552.
6. Fertilisation of orchids. Gard. Chron. **1861**: 831.
7. Vincas. Gard. Chron. **1861**: 831–2.
8. On the two forms, or dimorphic condition, in the species of *Primula*, and on their remarkable sexual relations. Journ. Linn. Soc., Bot. 6: 77–96.—Abst. in Gard. Chron. **1861**: 1048–9.
9. On the three remarkable sexual forms of *Catasetum tridentatum*, an orchid in the possession of the Linnean Society. Journ. Linn. Soc., Bot. 6: 151–7.—Abst. in Gard. Chron. **1862**: 334–5.—Transl. in Ann. des Sci. Nat., Bot. iv. **19**: 204–255.
10. On the various contrivances by which British and foreign orchids are fertilised by insects, and on the good effects of intercrossing. London, 1862, etc.
11. On the existence of two forms, and on their reciprocal sexual relation, in several species of the genus *Linum*. Journ. Linn. Soc., Bot. 7: 69–83.—Read Feb. 5, 1863.
12. On the sexual relations of the three forms of *Lythrum salicaria*. Journ. Linn. Soc., Bot. **8**: 169–196.—Read June 16, 1864.
13. On the character and hybrid-like nature of the offspring from the illegitimate unions of dimorphic and trimorphic plants. Journ. Linn. Soc., Bot. **10**: 393–437.—Read Feb. 20, 1868.
14. On the specific difference between *Primula veris*, Brit. Fl. (var. *officinalis* of Linn.), *P. vulgaris*, Brit. Fl. (var. *acaulis* Linn.), and *P. elatior* Jacq.; and on the hybrid nature of the common oxlip. With supplementary remarks on naturally produced hybrids in the genus *Verbascum*. Journ. Linn. Soc., Bot. **10**: 437–454.—Read Mar. 19, 1868.
15. The variation of animals and plants under domestication. London. 1868, etc. Index.

16. Notes on the fertilization of orchids. Ann. & Mag. of Nat. Hist. iv. 4: 141–159.
17. Fertilisation of *Leschenaultia*. Gard. Chron. Sept. 1871: 1166.
18. Fertilisation of the Fumariaceæ. Nature 9: 460.
19. The effects of cross- and self-fertilisation in the vegetable kingdom. London, 1876, etc.
20. The different forms of flowers on plants of the same species. London, 1877, etc.
21. Fertilisation of plants. Gard. Chron. n. s. 7: 246.
22. Fritz Müller on flowers and insects. Nature 17: 78.

DARWIN'S INFLUENCE UPON PLANT GEOGRAPHY AND ECOLOGY

PROFESSOR FREDERIC E. CLEMENTS
UNIVERSITY OF MINNESOTA

DARWIN dealt with plant geography only incidentally in connection with origin by descent. He was concerned chiefly with the bearing of migration upon community of origin, and consequently with the question of single and multiple origin of species. In his discussion of migration is found some consideration of barriers, endemism and isolation, but only in so far as these contribute to his main theme. On what might be called the ecological side proper, *i. e.*, the response of the individual, Darwin made his greatest contributions. Leaving apart his studies of pollination, movement and insectivorous plants, the ecologist must consider his fundamental work in variation and adaptation, together with his conclusions upon the questions inseparably connected with them, namely, competition, selection, inheritance of acquired characters and mutation.

In estimating Darwin's influence in all these matters, I have endeavored to keep in mind three view points: (1) his exact opinion upon each question, (2) his actual contribution to it, and (3) his share in our present knowledge of the subject, as well, perhaps, as his influence in shaping our present opinions where they do not rest on experimental knowledge. Several inherent difficulties have manifested themselves during this attempt. Chief among these is the impossibility of ascertaining what might be called the majority opinion of botanists, a difficulty aggravated by the fact that no two botanists would draw the same line between what is proved and what is merely held. In addition, Darwin's own views seem to have remained plastic to a degree not always evident in his most widely read books. This has brought the curious result that his earlier views have often had much the greater

influence in moulding opinion, while his later views are more in accord with scientific knowledge. Furthermore, it must be borne in mind that Darwin was the great apostle of origin by descent. It was his unique mission to bring the scientific world to accept this doctrine, a task of such magnitude that methods of origin, for the time at least, were relatively unimportant. In attempting to determine Darwin's actual contribution, one is confronted by the task of deciding how much credit is to be given to the discoverer of a new idea or principle, and how much to him who applies it and establishes it. It is fairly well known that Darwin was not the first to formulate the principle of evolution. Even in regard to natural selection, often accepted as distinctly Darwinian, Darwin himself has shown that he was anticipated by three other writers. Yet the fact remains that Darwin has contributed more to the foundations of biology than all of his forerunners.

A careful rereading of the "Origin of Species" and the "Variation of Animals and Plants under Domestication" has been found necessary to make Darwin's views emerge clearly from the mists of tradition and of recollection. It has seemed desirable also that he should himself speak in his own words, without the handicap of paraphrase and of the personal equation. Together with the manifest difficulty of making accurate and definite statements of the consensus of botanical opinion on mooted questions, this necessarily results in a more or less fragmentary and detached account of such a vast field.[1] Its value lies wholly in recalling to us Darwin's actual views without interpretation or emendation, so that each may determine for himself what part Darwin's work plays in his own views, and in botanical opinion as he sees it.

Distribution

Darwin formulated three laws of distribution: (1) "Neither the similarity nor the dissimilarity of the in-

[1] The references given after the various excerpts are to the sixth edition (1872) of the "Origin of Species," and to the second edition (1875) of the "Variation of Animals and Plants under Domestication."

habitants of the various regions can be wholly accounted for by climatal or other physical conditions," (2) "barriers of any kind or obstacles to free migration, are related in a close and important manner to the differences between the productions of various regions," (3) "the affinity of the productions of the same continent, or of the same area, though the species themselves are distinct at different points and stations."[2] These scarcely need comment, for they arise clearly from the law of origin by descent. They are such an intrinsic part of the foundation of plant geography as to require an effort to recognize the fact that it was once necessary to formulate them.

Single and Multiple Origin

From the very nature of his task, Darwin was forced to assume that species were first produced at one spot. To-day the fact that the same species may arise at two or more distinct places merely strengthens the law of descent, but in Darwin's time this would have greatly increased the difficulty of supporting his doctrine by the evidence drawn from the distribution of plants. Darwin's views upon this question were far from uncertain, as the following excerpt indicates.

> It is obvious that the individuals of the same species, though now inhabitating distant and isolated regions, must have proceeded from one spot, where their parents were first produced. We are thus brought to the question which has been largely discussed by naturalists, namely, whether species have been created at one or more points of the earth's surface. Undoubtedly there are many cases of extreme difficulty in understanding how the same species could possibly have migrated from some one point to the several distant and isolated points where now found. Nevertheless, the simplicity of the view that each species was first produced within a single region captivates the mind. He who rejects it, rejects the *vera causa* of ordinary generation with subsequent migration, and calls in the agency of a miracle.[3]

This view seems to be little more than an inheritance from the special creationists. It doubtless reflects the prevailing opinion of Darwin's time, and probably is in

[2] "Origin," 2: 129.
[3] "Origin," 2: 135.

accord with the consensus of opinion at present. What the current opinion is can only be a matter of conjecture, but notwithstanding the proofs of multiple origin afforded by adaptation and mutation, it would seem that the majority of botanists and nearly all zoologists still adhere to the doctrine of single origin.

MIGRATION

Darwin's treatment of migration is limited to evidence of the possibility of distant and occasional migration as the explanation of the many puzzles of distribution. It is evident that his position in regard to single origin caused him to turn to migration as the necessary solution of all the problems of distribution. His attitude upon both questions is shown by the following statement:

> Whenever it is fully admitted, as it will some day be, that each species has proceeded from a single birthplace, and when in the course of time we know something definite about the means of distribution, we shall be enabled to speculate with security on the former extension of the land.[4]

His experiments upon the carriage of seeds and fruits by ocean currents and by birds, though necessarily crude and simple, are classic. They still serve to indicate one of the really fundamental points of attack in the detailed quantitative study of migration.

VARIATION

A brief summary of Darwin's views upon variation is an impossibility. Under the headings "Causes of Variation," "Habitat as Cause," "Use and Disuse," I have assembled his own statements to make clear his position. These seem to differ in some essentials from the views often ascribed to Darwin, or at least held by many who regard themselves as his followers. They appear to be more in accord with the views of the ecologist who looks to the habitat for the final explanation of all changes, than with the opinions held by biologists in general. They show Darwin to have been much more in sympathy with

[4] "Origin," 2: 140.

Lamarck and Saint-Hilaire than he was himself aware. He thus becomes the connecting link between these two great but less appreciated seers, and the investigators of to-morrow whose success will rest on the experimental study of the habitat as the primary cause.

Causes of Variation.

I have hitherto sometimes spoken as if the variations so common and multiform with organic beings under domestication, and in a lesser degree under nature—were due to chance. This, of course, is a wholly incorrect expression, but it serves to acknowledge plainly our ignorance of the cause of each particular variation.[5]

No doubt each variation must have its efficient cause, but it is as hopeless to discover the cause of each as it is to say why a chill or a poison affects one man differently from another. Even with the modifications resulting from the definite action of the conditions of life, when all or nearly all the individuals which have been similarly exposed, are similarly affected, we can rarely see the precise relation between cause and effect.[6]

We must . . . conclude that organic beings, when subjected during several generations to any change whatever in their conditions, tend to vary: the kind of variation which ensues depending in most cases in a far higher degree on the nature or constitution of the being, than on the nature of the changed conditions.[7]

Those authors that adopt the latter view—that variability must be looked at as an ultimate fact, would probably deny that each separate variation has its own exciting cause. Although we can seldom trace the precise relation between cause and effect, yet the considerations presently to be given, lead to the conclusion that each modification must have its own distinct cause, and is not the result of what we blindly call accident.[8]

Habitat as Cause.

With respect to what I have called the indirect action of changed conditions, namely, through the reproductive system being affected, we may infer that variability is thus induced, partly from the fact of this system being extremely sensitive to any change in the conditions. Many facts clearly show how eminently susceptible the reproductive system is to very slight changes in the surrounding conditions.[9]

Changed conditions of life are of the highest importance in causing variability, both by acting directly upon the organization, and indirectly by affecting the reproductive system. It is not probable that variability is an inherent and necessary contingent under all circumstances.[10]

[5] "Origin," 1: 164. [6] "Variation," 2: 273.
[7] "Variation," 2: 229. [8] "Variation," 2: 232. [9] "Origin," 1: 10.

These several conditions alone render it probable that variability of every kind is directly or indirectly caused by changed conditions of life. Or, to put the case under another point of view, if it were possible to expose all the individuals of a species during many generations to absolutely uniform conditions of life, there would be no variability.[11]

We have good reason to believe, as shown in the first chapter, that changes in the conditions of life give a tendency to increased variability, and in the foregoing cases the conditions have changed, and this would manifestly be favorable to natural selection, by affording a better chance of the occurrence of profitable variations.[12]

Use and Disuse.

It is notorious, and we shall immediately adduce proofs, that increased use or action strengthens muscles, glands, sense-organs, etc., and that disuse, on the other hand, weakens them.[13]

There can be no doubt that with our anciently domesticated animals, certain bones have increased or decreased in size and weight owing to increased or decreased use. With animals living a free life and occasionally exposed to severe competition, the reduction would tend to be greater, as it would be an advantage to them to have the development of every superfluous part saved.[14]

Competition

In spite of the importance Darwin assigned to competition, for to him it usually comprises the whole process of natural selection, he gave little thought to its analysis and almost none to its investigation. His ideas of competition were drawn largely from Lyell and Herbert, and he was content to take it as a universal and fundamental process among living things, without detailed inquiry into its working or its precise relation to the origin of new forms. Darwin's actual contribution rests chiefly upon his formulation of the following law of competition, which recent quantitative experiments indicate to be fundamental:

As species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them if they come into competition with each other, than between the species of distinct genera.[15]

[10] "Origin," 1: 49.
[11] "Variation," 2: 234.
[12] "Origin," 1: 100.
[13] "Variation," 2: 276.
[14] "Variation," 2: 280.

Competition has, however, been almost completely neglected until the ecologist has begun the investigation of it in the last few years, and there are few subjects in which botanical opinion is so completely unformed.

Inheritance of Acquired Characters

Darwin's opinions upon this subject appear to have been modified little with time, contrary to the case with other views. Here again he was in almost complete accord with Lamarck and Saint-Hilaire, but he seems to have had little effect upon current opinion, especially among zoologists. The experimental ecologist would doubtless follow Darwin in regarding the inheritance of acquired characters as proved beyond question. Indications are not lacking that more and more botanists are coming to the same point of view. Darwin's attitude may be summed up in the following:

> The increased use and disuse of various organs produces an inherited effect.[16]
>
> With plants, the period of vegetation is easily changed, and is inherited, as in the case of summer and winter wheat, barley and vetches.[17]
>
> Changed habits produce an inherited effect, as in the period of the flowering of plants when transplanted from one climate to another.[18]
>
> Habit is hereditary with plants, as in the period of flowering, in the time of sleep, in the amount of rain requisite for seeds to germinate, etc.[19]
>
> Perhaps the correct way of viewing the whole subject would be to look at the inheritance of every character whatever as the rule, and non-inheritance the anomaly.[20]

Mutation

Darwin's attitude towards the sudden appearance of striking variations, of sports, and monstrosities towards what is now called mutation, is one held by the majority of American botanists to-day. To the latter, DeVries has supplied the scientific proof of origin by sudden and striking variation, but only a small number, the followers of DeVries, regard mutation as the fundamental or uni-

[15] "Origin," 1: 93.
[16] "Variation," 2: 273.
[17] "Variation," 2: 285.
[18] "Origin," 1: 12.
[19] "Origin," 1: 173.
[20] "Origin," 1: 15.

versal process. Zoologists, it would seem, incline to look with greater favor upon mutation as the regular method of origin.

At long intervals of time, out of millions of individuals reared in the same country and fed on nearly the same food deviations of structure, so strongly pronounced as to deserve to be called monstrosities, arise; but monstrosities cannot be separated by any distinct line from slighter variations. All such changes of structure, whether extremely slight or strongly marked, which appear amongst many individuals living together, may be considered as the indefinite effects of the conditions of life on each individual organism.[21]

Some naturalists have maintained that all variations are connected with the act of sexual reproduction, but this is certainly an error: for I have given in another work a long list of "sporting plants," plants which have suddenly produced a single bud with a new and sometimes widely different character.[22]

Some variations useful to man have probably arisen suddenly, or by one step.[23]

No one supposes that our choicest productions have been produced by a single variation from one stock.[24]

It may be doubted whether sudden and considerable deviations of structure such as are occasionally seen in our domestic productions, more especially with plants, are ever permanently propagated in a state of nature.[25]

I saw also that the preservation in a state of nature of any occasional deviation of structure, such as a monstrosity, would be a rare event, and that if first preserved, it would generally be lost by subsequent intercrossing with ordinary individuals.[26]

ADAPTATION

Darwin recognized the three fundamental methods of origin in nature, namely, variation, mutation and adaptation. It seems probable that to mutation he assigned its approximate value. In the "Origin of Species," variation with selection was given the preeminent place, and adaptation a minor one. Later, adaptation assumed greater importance to his mind, and there is some evidence that he may have assigned to it a value greater than that of variation. He had come to see more clearly that natural selection operated upon things already produced,

[21] "Origin," 1: 9.
[22] "Origin," 1: 11.
[23] "Origin," 1: 34.
[24] "Origin," 1: 37.
[25] "Origin," 1: 52.
[26] "Origin," 1: 111.

and to catch a glimpse of the fact that indefinite action, *i. e.*, variation, and definite action of the habitat, *i. e.*, adaptation, were at bottom the same thing.

His changing view point is recorded in his letters, and hence his later views are not generally known. As a result, scientific opinion has been more or less stereotyped in the well-known statements of the "Origin of Species" and has maintained in greater or less degree a position which Darwin himself had forsaken. Darwin's later opinions upon adaptation, as upon the causes of variation, and upon the inheritance of acquired characters, did not differ essentially from those of Lamarck. More important than this, for Lamarck was a prophet, not an investigator, they are in accord with the first results of the application of exact ecological methods to the question of the origin of new forms in natural habitats.

As far as I am able to judge, after long attending to the subject, the conditions of life appear to act in two ways—directly on the whole organization or on certain parts alone, and indirectly by affecting the reproductive system.[27]

In looking at many small points of differences between species, which, as far as our ignorance permits us to judge, seem quite unimportant, we must not forget that climate, food, etc., have no doubt produced some direct effect.[28]

In all cases, there are two factors, the nature of the organism, which is much the most important of the two, and the nature of the conditions. The direct action of changed conditions leads to definite or indefinite results. In the latter case, the organization seems to become plastic and we have much fluctuating variability. In the former case, the nature of the organism is such that it yields readily when subjected to certain conditions, and all or nearly all the individuals become modified in the same way. It is very difficult to decide how far changed conditions, such as climate, food, etc., have acted in a definite manner. There is reason to believe that in the course of time the effects have been greater than can be proved by clear evidence.[29]

The greatest mistake I made was, I now think, I did not attach sufficient weight to the direct influence of food, climate, etc., quite independently of natural selection. When I wrote my book, and for some years later, I could not find good proof of the direct action (*i. e.*, in producing definite variations) of the environment upon the species. Such proofs are now plentiful.[30]

[27] "Origin," 1: 8.
[28] "Origin," 1: 104.
[29] "Origin," 1: 165.
[30] "Life and Letters," 3: 159, 1876.

DARWIN'S WORK ON MOVEMENT IN PLANTS

PROFESSOR HERBERT MAULE RICHARDS
COLUMBIA UNIVERSITY

IT is remarkable, when one considers the central interest of Darwin's life, that he should have found time and strength to devote so considerable a portion of his energy to purely botanical work. It is natural and fitting at this time that the major interest of the world should be directed to his larger achievements, but it should not be lost sight of that his botanical work alone represents no small labor accomplished. We may indeed not always agree at present with his conclusions and may differ even as to actual observations, but the fact remains that he developed a number of highly important topics relating to plant behavior.

His lines of investigation among plants were indeed somewhat special, for he made no pretence of covering completely the field of even that side of botany which interested him, but simply investigated certain more or less important phases of plant life that came under his notice. It may be expressed, perhaps, by saying that his botanical studies were his avocation, and were employed by him in a measure as a recreation from the exactions exercised by his larger tasks. That does not mean, however, that there was anything dilettantish in the spirit of his attack on botanical problems or that his work along these lines was not as thorough as his circumstances permitted. Thoroughness indeed was an important element in all that Darwin undertook and the patient application to even small details is the secret of much of the value of these botanical studies.

From his published letters it would seem that his work with plants was to him of the nature of a pastime, serious indeed but none the less a pastime, in which he often found himself so interested that all other lines of

intellectual activity were for the time forgotten. Possibly what first inclined him to study plants was the delight of observation and experiment to which he so keenly reacted, for, placed as he was in the country and in none too good health, these faculties found their easiest and most natural outlet in his garden. Even when he was least well, so long as he was able to exert any effort at all, his plants claimed his interest and one of his friends speaks of how in the daily walk about the garden path there was always some experiment or some particular plant which was to be watched and noted.

He did not himself make any claim to being a trained botanist and, without in any way reflecting upon the value of the work which he did, it must be admitted that he was not. He freely asked help of his botanical friends and freely it was given.

Most of his botanical contributions were published in book form and it is to be noted that they had a relatively wide circulation for books of a special character, a fact which speaks well for the manner of treatment and general interest of the subjects about which he wrote. Of these works there are three which especially concern the subject of this address and these are as follows: "Insectivorous Plants" published in 1875, "The Movements and Habits of Climbing Plants" which appeared first in 1865 in the *Journal of the Linnean Society* and was afterwards printed in book form, and "The Power of Movements in Plants" which bears the date of 1880. It is not the intention to take these up seriatim or discuss each detail, but rather to point out what seem some of the more important and crucial aspects of the various subjects treated therein.

Perhaps the most important single fact that Darwin elucidated was that of the universality of the oscillations of the growing points of plant members. This he termed circumnutation, a word now generally adopted; and by it he meant the swinging motion of plant extremities as they progress through space, due to inequalities of

growth. He was not indeed the first to observe individual instances of either periodic or ephemeral movements of a more or less pronounced degree, but to him belongs the credit of first insisting upon the fact that all growing organs describe a more or less spiral orbit. He developed this idea with such enthusiasm that he carried his line of thought to extremes and concluded that all plant movements were but modifications and adaptations of circumnutatory motions. Only in the cases of the motions of Mimosa leaves and Drosera tentacles did he express his doubt as to the applicability of the principle of circumnutation to all plant movements. He included all forms of tropisms, contact responses, other than those named, under this one head. In the final chapter of "The Power of Movement in Plants" he says:

> It has been shown that the following classes of movement all arise from modified circumnutation, which is omnipresent whilst growth lasts, and after growth has ceased, whenever pulvini are present. These classes of movement consist of those due to epinasty and hyponasty,—those proper to climbing plants, commonly called revolving nutation, the nyctitropic or sleep movements of leaves and cotyledons, and the two immense classes of movement excited by light and gravitation.

In the next paragraph he excepts the contact movements of Mimosa and Drosera, already referred to, saying:

> Although so many movements have arisen through modified circumnutation, there are others which appear to have a quite independent origin; but they do not form large or important classes.

When we consider the nature of the man and reflect that the whole trend of his mind was towards the concept of unity in the organic world it does not seem extraordinary that he should have taken such an attitude; an attitude too that was helped on by the extreme simplicity of his methods of experimentation. The very fact that he approached the question with a mind entirely free from bias had its advantages, but it also brought a greater chance of being too easily swayed by his own point of view. It must be remembered also that the distinction be-

tween autonomous and induced or paratonic movements was not so sharply drawn then as it is now. At present we place the tropistic movements due to whatsoever external cause, under the general class of aitonomic movements, in contradistinction to circumnutation, epinasty, hyponasty and so forth, which we are pleased to term autonomic or due to internal causes. In the latter class, it must be confessed, the relegation of movements to autonomous causes is often a mere confession of ignorance, as is well instanced by the older opinion first advanced by Darwin that the twining of stem climbers is wholly autonomic. It is only in the sense that the movements of fixed plant organs are in the vast majority of cases ultimately due to unequal growth changes that we can say that circumnutation is the fundamental process concerned. In other words, it is only if we were to define circumnutation as the power of plant parts to show either unequal turgescence or unequal growth that we could accept the universality of Darwin's statement.

As far as his observations on circumnutation proper are concerned, or, as he would have termed it, unmodified circumnutation, his conclusions are of the highest value, and form even to the present day really a large part of our literature on the subject. By the simplest means he plotted the orbits, so to say, of a very considerable number of growing tips. Entirely aside from any especial interpretation to be placed upon them, his descriptions of the behavior of seeds during germination and of the growth of seedlings, give a clear and accurate account of the general organography of the adolescent plant.

In another very important direction were the researches of Darwin rewarded by far-reaching results; namely, in the matter of the transmission of stimulus in plants. Until the publication of his experiments it had been largely overlooked that there might be a separation in space between the percipient and motor zone in tropic responses. It is true, no doubt, that some of his methods

and even some of his conclusions were faulty, but nevertheless the credit belongs to him for establishing a point of departure from which further developments of first importance have come. The demonstration of so fundamental a fact has had no inconsiderable influence in the understanding and interpretation of sense perception among plants.

Although many observers at first contended against the possibility of such a propagation of stimulus and denied the accuracy of Darwin's results, yet the general correctness of his statements has been established even though differences in interpretation may have crept in. One reason, no doubt, why it was difficult to admit and support Darwin's conception and to corroborate his results, is that the region capable of perceiving a stimulus is so localized and the conduction to the responsive area is over so short a distance. One may gather from his writings that he did not regard the response to stimuli in the nature of a release of a regulatory mechanism, as it is now so commonly understood: his point of view indeed as to the nature of such tropic responses as being merely a modified form of circumnutation was against such an interpretation. His attitude was of course that of the teleologist, for he was ever keen to uncover purpose in the reaction of organisms. In his concluding remarks and summaries, while he suggested the interpretation of such responses along the line of consciousness he exhibited a considerable reserve and went no farther than indicating the appropriateness of a comparison of the similarity to the responses in lower animals. He did not enter largely into the somewhat fruitless field of the philosophical discussion of the question. His reserve possibly but reflects the greater caution of a past generation in interpreting protoplasmic response universally in terms of what we know about the problem in higher animal forms, but be that as it may, one is inclined to the opinion that it was Darwin's own reluctance to commit himself too unreservedly which restrained him, for in

other matters he has amply shown that he was not afraid to combat what to him were mere conventionalities.

A large portion of his book on climbing plants is devoted to a consideration of the tendril bearers and takes up a wide range of forms. The exceeding sensitiveness of these organs to contact Darwin was one of the first to appreciate, but he went somewhat astray in supposing that mere pressure was enough to induce the characteristic coiling response. It was not thoroughly understood until later that weight alone is not sufficient, but that the stimulus must involve some more intricate contact shock. He did not understand that the exciting body must have a certain degree of what one may call roughness and consequently he did not understand the inaction of tendrils to raindrops.

His conclusions did not wholly agree with the now accepted explanations of the nature of the response of tendrils but it inclined to the view that the rapid reply of incurving tendrils was primarily caused by turgor changes ultimately rendered permanent by growth. More recently it has again been claimed that the curvature is wholly a growth phenomenon, but in so much as turgor changes are often apparently so greatly concerned with the first stages of cell enlargement incident upon growth, may not the initial curvature be after all a matter of unequal turgor pressure on the two sides of the tendril? Here as in other places Darwin considered the response of contact stimulus a form of modified nutation.

Although Drosera and similar plants were not considered by Darwin in this connection, in so much as some phases of his study had to do with their response to contact irritation, it is suitable to introduce the matter now. His investigation of the behavior of Drosera was especially detailed and represented at the time a great advance in the knowledge of the habits of this insectivorous form. There is not, as a matter of fact, any more elaborate or complete study at present, although his results were published some thirty years ago. Many important

observations were made by him, especially that the gland at the tip of a tentacle is exclusively the sensitive region and that a stimulus can be propagated down the central tentacles and along to and up the adjacent ones. Although he made most careful and repeated examination of the protoplasmic behavior as the stimulus progressed, and noted some curious changes which take place in the protoplasm of the responding tentacles, yet he was unable to advance any explanation of the physics of the process. Indeed, none has been offered since and much that Darwin said is still the last word on the subject.

Extending his work from the effect of mechanical stimuli to chemical ones, Darwin showed that many substances of very various kinds could effect a very vigorous response. He was, indeed, the first to make an endeavor at a close study of the insectivorous or rather carnivorous plants. Not only were his observations on the inflection of the tentacles of Drosera and the trapping of insects by this and other forms largely new; but also, and what was more important, perhaps, his investigations into the digestive action of their secretions were really the first in the field. His experiments along this line were especially exhaustive; and, with the exception of some details later writers have done little by way of correction or amendment. He did not it is true, isolate any specific enzymes but nevertheless we came to the conclusion that a pepsin-like enzyme was excreted by these plants, which enables them to digest external proteid material. He also noted the rennet-like action of the excretion in Drosera and arrived at the just conclusion that the curdling of milk due to the latter could not come from the acidity of the excretion alone, though at that time little or nothing was known concerning vegetable rennets. It is not to be wondered, when one considers the lesser acquaintance which was then possessed of ferments in general and plant enzymes in particular, that Darwin did not further discuss or attempt to investigate the enzymes which he had discovered and to determine whether they

were peptic or tryptic or whether the curdling power was due to a specific enzyme, apart from the others.

The complexity of ferment action and the possible co-existence of several distinct enzymes in one secretion was not fully appreciated at that time, and working as Darwin of necessity did, he was not in close enough touch with these matters as they then stood to branch out on his own account into very new fields. What he did do was to make a careful and pretty exhaustive empirical study of the action of the excretion of the glands on a great range of substances. If his list of the latter included a number which were immaterial by way of affording new light on the question and a few which, owing to their mode of preparation, gave inconclusive or erroneous results, it matters very little. He proved successfully the main thesis which he maintained, namely, the ability of these insectivorous plants to avail themselves of proteids as food. When one considers how much even to-day in the study of enzymes depends on almost pure empiricism and what valuable results have in the past been obtained by such methods, one does not cavil at Darwin's mode of attack, although at times it may impress one as a bit happy-go-lucky.

As a detailed study of the habits of an organism his extended observations on Drosera stand out as a masterpiece of this kind of work and the collective result of this work may justly be regarded as one of his best pieces of botanical investigation. It is evident from his letters that he took the keenest interest in this plant, which apparently stimulated his imagination and his desire towards investigation as much as any one thing which came under his notice. It was a subject peculiarly well fitted for his type of investigation, for in it he did not require elaborate mechanical aid to arrive at important results and the previous literature on the subject was scanty and for the most part of minor importance. He had an almost clear field and made the most of his opportunity by producing a work which must for all time re-

main the basis of our knowledge of these interesting forms. He pushed it as far as his means at hand permitted, and while in many points he could not arrive at definite conclusions, it is a fact that most of his unanswered questions are unanswered still. While his knowledge of plant physiology may not have been broad enough for him to correlate this special form of nutrition, with the general problems of plant metabolism it is to be remembered that after all it was not from such a standpoint that he took up the problem.

There is one characteristic which is particularly admirable in all of Darwin's botanical work and that was his endeavor in so far as he could to examine an abundance of different forms which would illustrate any topic under investigation. This is the more to be remarked since he was not really very fortunately placed in the matter of obtaining material. For keeping his plants after he had obtained them he had to depend entirely upon such facilities as his own garden and greenhouse afforded. Being unable himself to collect material to any extent, he had to depend upon the generosity of his friends and correspondents, who, it may be said, responded with alacrity. None but one of very active mind and great perseverance would have accomplished what he did in an experimental way under the difficulties which beset him, and his work affords a good example of how a relatively large amount can be accomplished by even a little time given continuously. Entirely aside from any absolute value which these books may have, they were an important contribution at that stage in the development of plant physiology, to the literature on the subjects on which they touched. No man with a less well developed faculty for detail and continued effort could have kept the thread of the work so well, despite the many interruptions to which it was subjected. Their value, it may be said, is more to botanical science than a merely sentimental one—it is rather in many respects one of real achievement.

It has been stated that one of the greatest services rendered by Darwin to the study of natural history was the revival of teleology. The presence of this mode of thought in his work shows no better anywhere than in his work on the movements of plants, where it apparently afforded to him one of his liveliest interests. In the light of the present disfavor into which teleological interpretations have fallen these statements, which are indeed in accord with the mental attitude of Darwin, require some comment. It is not that one need raise one's voice in favor of teleology as such, to apologize for his purposeful explanations of the form and function of organs; but it should in justice be said that it is where teleological evidence and teleological reasoning are accepted as a finality or where they lead to prejudgment that the most mischief is done. Darwin's whole make-up and trend of thought was such as to make him turn to immediate causal explanations for natural phenomena and he unquestionably was a teleologist, but in the main his interpretations were tempered by common sense, intellectual reserve and balanced judgment. It has been rightly said, too, that his teleology had a far wider and more coherent plan than that of his predecessors and it may be added it was less positive than that of some of his contemporaries and some of those that followed him.

It is wholly natural that with a mind like his, which ranks him with the greatest correlaters and unifiers of loose facts that the world has known he should also have attempted to unify the explanations of the phenomena examined in his botanical researches and his position as to the fundamental nature of circumnutation was no doubt a result of his temperamental attitude towards large questions. But while we need not necessarily follow him in all of his generalizations the fact remains that he did no inconsiderable service to botanical science if in no other way than, at least, in showing what may be learned from the close and careful examination of the plant as a living organism.

In a final summing up of Darwin's studies that have come under discussion here, perhaps a fair statement may be made by saying that he investigated, as accurately as both his knowledge and his facilities for experimentation allowed, a large range of plant forms which illustrated the especial subjects in which he was interested; that he discovered or drew attention to many important facts, either previously unknown or neglected regarding the habits of the plant forms which he had under observation; that if his interpretations were at times faulty, his observations were in the main accurate; and that he revivified subjects which had often times become only of more or less academic interest. Darwin himself—none better—recognized that many of his experiments must be unsatisfactory and his explanations merely tentative; and he was ready enough to accept correction which appeared to him justified. The very fact that he brought to his botanical researches a mind fresh and unprejudiced lends a peculiar value to his work. Unhampered by tradition and with an open mind, he interpreted the facts as he saw them, and we must remember that some of our criticisms may be in part due merely to the greater complexity of our own interpretations, than to any absolute superiority of them. Despite the advances which have been made, it should not be forgotten that Darwin's influence was in the direction of sound investigation; and we should not pass over ungratefully this phase of plant physiology from which has come much that is of the first importance to-day. As a stimulus to later investigators Darwin's work, whether in botany alone or in other fields, has had a profound influence on the plant physiologist though he may not always recognize it. It would be our shame if we could not have improved over the concepts of the science as current in Darwin's time, and our misfortune if we think that these betterments are not capable of as relatively great advance in the future.

AN EXAMINATION OF DARWIN'S "ORIGIN OF SPECIES" IN THE LIGHT OF RECENT OBSERVATIONS AND EXPERIMENTS

PROFESSOR EDWIN LINTON

WASHINGTON AND JEFFERSON COLLEGE

ABOUT three years ago, some members of a local club, to which the writer belongs, having heard that Darwinism was on its death-bed, a report on the origin of species was ordered. The present paper is made up from notes prepared for that occasion.

In a letter to Hooker, March 9, 1885, Professor Huxley says:

> I have been reading . . . the book [Origin of Species] for the nth time. . . . It is one of the hardest books to understand thoroughly that I know of, and I suppose that is the reason even people like Romanes get so hopelessly wrong. ("Life and Letters," II, 204.)

If Huxley, who helped to fight Darwin's battles when "The Origin of Species" was young, who talked and argued with its author, can make such a statement concerning the book, it is little wonder that people come to different conclusions after reading it now.

My examination of Darwin's great work in the light of present-day beliefs has resulted in the finding of numerous passages which support the following theses:

1. Darwin's main thesis is the doctrine of descent as against the theory of the immutability of species.

2. A secondary thesis accounts for the origin of species by the theory of descent with modification through variation and natural selection.

3. Two kinds of variations are recognized: (*a*) Fluctuating variations as now understood, but including also variations of such a degree as would make steps in development as great as those which separate existing varieties. (*b*) Sudden changes, or sports.

It is to be observed that this classification of varieties

is not quite in agreement with the present-day distinction between fluctuating variations and mutations. Indeed, there are many who think that the distinction between the ampler fluctuations, on the one hand, and the lesser mutations, on the other, is not entirely established.

Darwin nowhere claims that natural selection is of the nature of a creative force.

I shall now cite a few passages in support of the above findings. References are made to the sixth edition. All italics are mine.

I. The main thesis is the origin of species by descent as opposed to the theory of the immutability of species or the independent creation of species.

While Darwin believed that varieties are incipient species he also believed that this identity had not yet been demonstrated. In speaking of the resemblance of varieties to species he says:

> Independently of the question of fertility and sterility, in all other respects there seems to be a general and close similarity in the offspring of crossed species and of crossed varieties. If we look at species as having been specially created, and at varieties as having been produced by secondary laws this similarity would be an astonishing fact. But it harmonizes perfectly with the view that there is no essential difference between species and varieties (pp. 261–2).

Again:

> It has been asserted over and over again by writers who believe in the immutability of species that geology yields no linking forms (p. 208).

And on page 290:

> Let us now see whether the several facts and laws relating to the geological succession of organic beings accord best with the common view of the immutability of species, or with that of their slow and gradual modification through variation and natural selection.

Also:

> This grand fact of the grouping of all organic beings under what is called the natural system is utterly inexplicable on the theory of creation (p. 413).

A few pages farther on he says:

> If species be only well-marked and permanent varieties, we can at

once see why their crossed offspring should follow the same complex laws in their degrees and kinds of resemblance to their parents, . . . as do the crossed offspring of acknowledged varieties. This similarity would be a strange fact if species had been independently created and varieties had been produced through secondary laws (p. 417).

On the following pages, 418–419, he summarizes facts such as the close resemblance between existing and extinct forms on the several continents, the inhabitants of oceanic islands, on islands near continents, and closes with this sentence:

> Such cases as the presence of peculiar species of bats on oceanic islands and the absence of all other terrestrial mammals, are facts utterly inexplicable on the theory of independent acts of creation.

I make but one more quotation in this connection. Near the end of the book, in a sentence which the careless reader might understand to refer to something like the modern mutation theory, he says:

> Under a scientific point of view, and as leading to further investigation, but little advantage is gained by believing that new forms are suddenly developed in an inexplicable manner from *old and widely different forms*, over the old belief in the creation of species from the dust of the earth (p. 424).

Such quotations could be multiplied many times, for over and over again throughout the book he speaks of his theory as standing for the mutability of species as against the independent creation of species. Indeed, so convincing to the world was Darwin's argument in support of his main thesis that the word Darwinism to the popular mind stands for the theory of descent, as it is perfectly right that it should do.

II. A secondary thesis is an attempt to account for the origin of species by the theory of descent with modification through variation and natural selection.

I shall now attempt to show by quotations:

1. Darwin's view of the part played by fluctuating variations.
2. The rôle of sudden variations.
3. The part taken by natural selection.

1. The following quotations would prove a narrow and

restricted meaning for the theory of descent with modification through variation if it were clear that Darwin always meant fluctuating variation when he used the word variation.

On page 156 he says:

> Why should not nature take a sudden leap from structure to structure? On the theory of natural selection we can clearly understand why she should not; for natural selection selects only by taking advantage of slight successive variations; she can never take a great and sudden leap, but must advance by *short and sure, though slow steps*.

In attempting to explain the puzzling phenomenon of the so-called neuter, really undeveloped female animals, he says:

> As natural selection acts only by the accumulation of slight modification of structure or instinct, each profitable to the individual under its conditions of life, it may reasonably be asked, how a long and gradual succession of modified architectural instincts, all tending towards the present perfect plan of construction, could have profited the progenitors of the hive-bee?

The answer to this query, by the way, begins with a sentence which has a very modern sound:

> This difficulty, though appearing insuperable, is lessened, or, as I believe, disappears, when it is remembered that *selection may be applied to the family, as well as to the individual, and may thus gain the desired end* (pp. 229–230).

The following utterance should be read with Darwin's main thesis in mind:

> If numerous species belonging to the same genera or families have really started into life at once the fact would be fatal to the theory of evolution through natural selection (p. 280).

Inferences have been drawn from the foregoing sentence as though Darwin had written: If numerous species, etc., have really started into life by variations greater than fluctuating variations, as that term will be understood at the beginning of the twentieth century, the fact would be fatal to the theory of evolution through natural selection.

Although, in his concluding chapter he makes use of such expression as:

. . . Complex organs . . . have been perfected . . . by the accumulation of innumerable slight variations.

He also says:

It is, no doubt, extremely difficult to conjecture by what *gradations* many structures have been perfected . . . (p. 404).

Again, on pp. 413–414:

As natural selection acts solely by accumulating slight successive, favorable variations, it can produce no great or sudden modifications; ***it can act only by short and slow steps.***

I think that it is evident from Darwin's discussion of varieties of oaks that he would not have regarded such work as that of DeVries on the evening primrose as making a revision of the foregoing sentence necessary. Even if DeVries's mutants are what he thinks them to be, that is, elementary species, still evolution of species by that means must be by "short, slow steps."

Even if it should be shown that species originate only by mutation, the following sentence might be permitted to stand:

New species have come on the stage slowly and at successive intervals, and the amount of change after equal intervals of time, is widely different in different groups (p. 417).

2. By the following quotations I shall attempt to show the rôle which that kind of variation, now called mutation, plays in the evolution of species according to Darwin's view.

When it is noted that DeVries makes use of facts recorded by Darwin in support of his views, it will be seen that there is some reason for suspecting that some of the facts which in Darwin's day were thought to be of the grade of fluctuating variations were really of the kind now believed by many to be something quite different.

On page 22 is this statement:

Some varieties useful to him (man) have probably *arisen suddenly, or by a step.*

Examples are cited, *e. g.*, the fuller's teasel, the turnspit dog, etc. DeCandolle's memoir on the oaks of the

world is alluded to. This gives the rank of species to the forms which differ by characters never varying on the same tree and never found connected by intermediate states. Out of 300 species at least two thirds are provisional species. Thus *Quercus robur* has twenty-eight varieties, all of which, excepting six, are clustered round three subspecies.

Commenting on this condition of things, that is, where there is no clear line of demarcation between species and subspecies, and between subspecies and varieties, or between lesser varieties and individual differences, he thus concludes:

> Hence I look at individual differences, though of small interest to the systematist, as of the highest importance to us, as being the first steps towards such slight varieties as are barely thought worth recording in works on natural history, and I look on varieties which are in any degree more distinct and permanent, as steps towards more strongly-marked and permanent varieties; and at the latter as leading to subspecies, and then to species (pp. 41–2).

A well marked variety may therefore be called an incipient species; but whether this belief is justifiable must be judged by the weight of the various facts and considerations to be given throughout this work (p. 42).

Darwin noticed that wide-ranging, much-diffused and common species vary most; also that species of the larger genera in each country vary more frequently than the species of the smaller genera; further, that many of the species included within the larger genera resemble varieties in being very closely, but unequally related to each other, and in having restricted range (pp. 42–45).

The following sentence is interesting in this connection:

> Every one who believes in slow and gradual evolution, will of course admit, that *specific characters may have been as abrupt and as great as any single variation which we meet with under nature or even under domestication.*

The above-quoted sentence follows a notice of Mivart's belief that new species manifest themselves with suddenness and by modifications beginning at once, of which Darwin says:

This view, which implies great breaks or discontinuity in the series, appears to me to be improbable in the highest degree (p. 201).

Such statements appear to be contradictory, until it is remembered that the kind of new species meant by Mivart would involve such violently sudden changes as the three-toed Hipparion giving rise immediately to the one-toed horse; or the wing of a bird suddenly appearing in place of the fore-limb of some dinosaur.

Indeed, it seems to be to be demonstrable that the statement of Darwin's views respecting variation requires but little change to bring them into harmony, or, at least, make them include, the origin of varieties by mutation.

By abrupt variations which are yet not greater than a single variety may show, he means such cases as the six-fingered Kelleia family, or the ancon ram. It is of this kind he is speaking when he says:

Excluding such cases of abrupt variations, the few which remain would at best constitute, if found in a state of nature, doubtful species, closely related to their parental types.

On the other hand, it is clear that he included under ordinary variations some, at least, which may now be called mutations. Thus:

Although very many *species have almost certainly been produced by steps not greater than those separating fine varieties;* yet it may be maintained that some have been developed in a different and abrupt manner. Such admission, however, ought not to be made without strong evidence being assigned (p. 203).

This is probably as good a place as any to call attention to the fact that in the title of the book the theory is not stated to be the origin of species by the natural selection of favored *individuals,* but by the natural selection of favored *races.* Morgan's term *the survival of species* does not appear to me to be any improvement on this. To my mind a still better statement is that which stands at the head of a syllabus of lectures by Professor James D. Dana, "On the Theory of the Origin of Species through Natural Causes."

Resuming the citations, the following explicit statement is illuminating:

By the theory of natural selection all living species have been connected with the parent species of each genus, *by differences not greater than we see between the natural and domestic varieties* of the same species at the present day; and those parent species now generally extinct, have in their turn been similarly connected with more ancient forms; and so on backwards always converging to the common ancestor of each great class (p. 266).

Here is a sentence which anticipates some recent speculations respecting a so-called plastic period in the life of a species:

It is a more important consideration, leading to the same result, as lately insisted on by Dr. Falconer, namely, that the period *during which each species underwent modification,* though long as measured by years, was probably short in comparison with that *during which it remained without undergoing change* (p. 279).

To the same purport is the following:

This gradual increase in number of the species of a group is strictly conformable with the theory, for the species of the same genus and the genera of the same family, can increase only slowly and progressively . . . *one species first giving rise to two or three varieties,* these being slowly converted into species, which in turn produce by equally slow *steps* other varieties and species . . . (p. 293).

Concerning the origin of varieties he has this to say:

The complex and little known laws governing the production of varieties are the same, so far as we can judge, with the laws which have governed the production of distinct species (p. 415).

In the following passage provision appears to be made for the origin of varieties by mutation:

I have now recapitulated the facts and considerations which have thoroughly convinced me that species have been modified, during a long course of descent. This has been effected chiefly through natural selection of numerous successive, slight favorable variations; aided in an important manner by the inherited effects of the use and disuse of parts, and in an important manner, that is in relation to adaptive structure, whether past or present, by the direct action of external conditions, *and by variations which seem to us in our ignorance to arise spontaneously.* It appears that I formerly underrated the frequency and value of these latter forms of variation, as leading to permanent modifications of structure independently of natural selection, . . .

He adds, in answer to certain recent criticisms that he placed at the end of the introduction to his first edition, the following words:

I am convinced that natural selection has been the main but not the exclusive means of modification (p. 421).

3. The following explicit statement makes it very clear that Darwin did not regard natural selection in the light of an originating cause:

Some have imagined that natural selection induces variability, whereas it implies only the preservation of such variations as arise and are beneficial to the being under its conditions of life (p. 63).

It would appear that Huxley, in 1860, thought that natural selection was being urged as an originating cause. He says:

It is not absolutely proven that a group of animals having all the characters exhibited by a species in Nature has ever been originated by natural selection, whether artificial or natural.

He also thought that Darwin embarrassed himself by the use of the aphorism, *natura non facit saltum;* that nature does make a jump now and then, and that a recognition of the fact is of no small importance in disposing of many minor objections to the doctrine of transmutation. In 1861, in a letter to Hooker, he says:

The great desideratum for the species question at present seems to me to be the determination of the law of variation. . . . Why does not somebody go to work experimentally, and get at the law of variation for some one species of plant?

In 1885 he was reading the "Origin of Species" and finding it one of the hardest books to understand that he knew. In 1888 he says in a letter to Hooker:

Darwin has left the causes of variation and the question whether it is limited or directed by external conditions perfectly open.

Writing to Bateson, February 20, 1894 (?), he says:

I see you are inclined to advocate the possibility of considerable "saltus" on the part of Dame Nature in her variations. I always took the same view, much to Mr. Darwin's disgust, and we used often to debate it.

In the light afforded by these comments of Huxley, and after a careful rereading of the "Origin of Species," I am inclined to the belief that in the brilliant work of Hugo DeVries we may have a key to a real understanding of the difficulties in question.

Huxley, with his tendency to reach conclusions quickly, which, he confesses, sometimes led him into mistakes, saw intuitively, let us say, that the beginning of varietal differences might be by a sudden leap. While Darwin, who reached conclusions only after careful examination of all possible contributing data, although realizing that the origin of species from variations, by natural selection had not been proved, thought that they furnished the most favorable material for natural selection to work upon. At the same time, I think that I have shown by means of numerous quotations from the "Origin of Species" that the very slight changes which DeVries has shown to mark the beginning of some varieties, while recognized by Darwin, were thought of by him as of the same order as ordinary (now called fluctuating) variations. This view is justified, I think, by his frequent use of the word *step*. Possibly this explains why Huxley found the book such a hard one to understand thoroughly. It also throws some light on the unsatisfactory condition in which Darwin is supposed to have left the question of the origin of varieties. To my mind, instead of this being a blemish on Darwin's work, as it seems to be held by some recent writers, it is, when the state of biological knowledge in his day is taken into account, in harmony with his known caution and sagacity. To blame him for not making a sharp distinction between fluctuating varieties and mutations would be like finding fault with Copernicus for not knowing what Kepler and Newton discovered, or criticizing Newton harshly because his theory of light left much for subsequent workers before the electro-magnetic theory was possible.

THE DISTINCTION BETWEEN DEVELOPMENT AND HEREDITY IN INBREEDING

DR. EDWARD M. EAST

THE CONNECTICUT AGRICULTURAL EXPERIMENT STATION

THERE is among animal breeders a tendency to frequent out-crossing as a preventive of a feared deterioration of the breed through inbreeding. This fear is of long standing, probably having arisen contemporary with, or as a result of, the repugnance to incest possessed by so many human tribes. This general state of mind on the ethical question has brought about an unwarranted belief that there is a physiological law opposed to inbreeding *per se*. Inbreeding undoubtedly results in many cases of deterioration, but the success of the few daring spirits that have inbred superior stock shows that the cases of deterioration were merely made possible by the course pursued, and were not its direct and constant result.

In the vegetable kingdom a slightly different state of affairs obtains. Some species thrive under inbreeding while others appear to deteriorate. Maize is reduced in vigor in one generation, so that the difference between selfed and crossed plants is noticeable in seedlings two weeks old. Other natural species have evolved intricate mechanisms whereby they are perpetually self-fertilized, and some have even given up sexual reproduction for parthenogenesis (Taraxacum), and yet have survived in competition by their hardiness and prolificacy. Darwin even found that in species that generally appeared to be injured by inbreeding (*Ipomœa purpurea* and *Mimulus luteus*), individuals were occasionally produced that were not affected.

The classical researches which included the above observations are familiar to all. Direct comparison of crossed and selfed plants, and investigations into the mechanical means by which plants are cross-fertilized,

all pointed to the truth of the dictum "Nature abhors perpetual self-fertilization," which, by the way, simply corroborated the results that Knight had obtained a half century before. That there are important exceptions to this rule was recognized, however, and Hays,[1] arguing from the case of wheat, suggested that it be changed to read: "Nature abhors a radical change which would require species to cross in much closer or in much more radical relationship than is their long established habit." Each of these sayings is probably correct as far as it goes. Nature does seem to have provided more for cross-fertilization than self-fertilization. Yet the very fact that all species do not cross-fertilize naturally, shows that although cross-fertilization may be a desirable thing—a thing to be provided for by nature—it does not follow that inbreeding and decrease in vigor hold the relation of cause and effect because they are often linked together.

As a matter of fact, the data that we possess regarding the supposed degeneration through inbreeding do admit an entirely different explanation, an explanation more compatible with contemporary knowledge. The hypothesis, first suggested by Shull,[2] is that the danger from self-fertilization in naturally cross-bred species *may be due simply to the isolation of biotypes*. It is an established fact, although the cause is unknown, that crosses between nearly related types (in both animals and plants) are usually more vigorous than either of the parent types alone. Since inbreeding tends to isolate types homozygous in their characters, these homozygous types, coming from species naturally crossbred, are thus deprived of the stimulus which came through free intercrossing and appear to deteriorate.

A little later the present writer[3] pointed out that a

[1] Hays, W. M. "Plant Breeding." Bull. U. S. D. A. Div. Veg. Phy. & Path. 29: 1901.

[2] Shull, G. H. "The Composition of a Field of Maize." *Ann. Rpt. Amer. Breeders' Assn.* 4: 1908.

[3] East, E. M. "Inbreeding in Corn," Ann. Rpt. Conn. Agr. Exp. Station, 1907–8.

reconsideration of the work of Darwin and others shows that it accords with this theory. As a single example from Darwin we may consider the experiments with *Ipomœa purpurea*, which were his longest, being carried on as they were for ten generations. If an actual degeneration were taking place it might be expected that the difference in height between the crossed and the selfed plants should have gone on increasing in the later generations. Such was not the case, however, and Darwin himself remarked upon it. Nevertheless, the results obtained were what should have been expected by the hypothesis just given, for after a few generations even the crossed plants in such a small lot would have become more or less inbred, and would have approached the inbred stock in size. In further support of this view it is noticeable that the crossed flowers varied in color in the earlier generations, but became more uniform toward the end of the experiment, while the selfed plants were uniform in color throughout the whole time. This, then, explains why his out-crosses with other stock showed greater vigor than did cross-fertilization within a type, the latter strain having become more nearly identified with the selfed plants through continued close breeding.

Such results as the above from Darwin, my own experiments with maize and tobacco, together with the ready agreement of the facts in other breeding work with which I am familiar, indicate that this problem of degeneration combines two questions; the one a question of heredity, the other a question of development. Davenport[4] has recently called attention to what I consider the former question, suggesting that deterioration through inbreeding may be due to the isolation of homozygous recessives, or the combination of recessive di-hybrids. This is undoubtedly true when the allelomorphic pair under consideration is the presence and absence of something essential to the normal development of the organ-

[4] Davenport, C. B. "Degeneration, Albinism and Inbreeding." *Science*, N. S., 28: 454, 455, 1908.

ism. But the principle will probably be found to apply also where there is presence of an abnormal dominant character. We do not know many such characters at present, but susceptibility to rust in wheat and congenital cataract in man may be cited as approaching our meaning.

The instances where the presence or absence of evil qualities is brought to notice through their isolation by inbreeding are few in number, however, and can not account for the large number of cases where there is a loss of vigor by this means.

Let us consider just what this deterioration, so-called, is. Does it represent an actual degeneration in hereditary characters? In general it does not. Darwin's experiments consisted mainly in comparing heights of plants. His measure of vigor, then, is a measure of rapidity and amount of cell division. In no cases does he speak of losses of characters, and seldom of disease. Even where disease appeared, it usually appeared alike in inbred and cross-bred plants. In my own experiments, I have observed some twenty-five families of maize inbred for two generations, and a lesser number through the fourth generation, and have not found a single sign of degeneration. In all characters of stalk, leaves, roots, male inflorescence, female inflorescence, and mature seed, the plants were normal. It is merely in the matter of size of plant and ear, and thereby yield, that the plant compares unfavorably with cross-bred plants.

Further, there is no *continuous* decline in yield as should be expected in actual degeneration. There is somewhat greater difference between fourth generation inbred and cross-bred plants than there is between those of the second generation. This last fact may be explained by considering the frequency with which heterozygotes in certain characters are selected even in the most careful work. Not all character pairs can be kept under observation, and from the mere fact of its being inbred we can not presume that the isolation of a homozygous strain is complete. The past summer one of our

fourth-year inbred families was found to be heterozygous in the character pair presence and absence of color in the silk. But there is absolutely no indication that there is loss of vigor *after* the isolation of a homozygous individual.

It seems, then, that this type of degeneration (the common type) is limited to a partial loss of power of development, a reduction in rapidity and amount of cell division. The phenomenon is readily apparent in open fertilized plants like maize, for there the vigorous growing hybrids are continually being formed in nature. When the components of these hybrid strains are isolated by inbreeding, reduction in vigor is immediately seen. In plants like tobacco, which are naturally inbred, no degeneration is suspected, for the natural plants are taken as the standard. There is an increase in vigor, however, when inbred tobacco strains are crossed, and if the F_1 generation is then taken as a standard, there is a loss of vigor through inbreeding comparable to that which takes place in maize.

Upon what theoretical basis can these facts rest? In the first place, whether or not we accept the theory that the nucleus is the bearer of all hereditary characters, nevertheless we must believe that amphimixis has two functions, the one a recombination of hereditary characters, and the other a stimulation to development. If we postulate that there is an increase in this stimulation when two strains differing in gametic structure are combined, we satisfy all observed conditions. This will explain why *decrease in vigor* and not *degeneration of characters* is usually the sole effect of inbreeding, and will also show why this decrease must reach a limit with the complete isolation of an individual homozygous in all characters, and never will result in a complete degeneration, or "running out," of the strain. One other effect sometimes noticed in inbreeding is also thoroughly in accord with the hypothesis. This is decrease in fertility. Since fertility must necessarily start with the union of

the gametes and their subsequent division, a decrease in this stimulation in species which have for ages depended upon cross-fertilization may result in decreased fertility.

We can scarcely form a definite idea of the mechanism through which such a stimulation may take place. There may be chemical compounds found in different strains that react when brought together. If this were the case we should expect to find separate families with like "compounds" which when crossed would not be more vigorous than when inbred. It would be difficult to establish such a thing experimentally. On the other hand, the actual fact of difference[5] in gametic constitution may set up a biological "action" analogous to ionization. If this were true, and individuals of the F_1 generation heterozygous in all differentiating characters were selected in succeeding generations, there should be no reduction in vigor, while individuals of the F_2 generation, homozygous in their characters, should compare in vigor to the P_1 generation. This hypothesis we are testing, but results will necessarily be slow.

The F_1 generation of thirty maize crosses were grown in 1908 on well fertilized land in Connecticut. They were planted three feet six inches each way, about four stalks to the hill. Seeds from the same parent ears[6] which were used to make the crosses were also grown for comparison. Only fifty hills of each of the crosses and of each parent could be grown on account of limited space, but the soil conditions were such that a very fair

[5] The objection will be raised that beyond a certain amount of difference between gametes, there will be sterility. It is generally true that there is sterility with wide differences in botanical or zoological characters, but there are exceptions, and we must not fall into the same old rut of putting the two down as cause and effect because there is at present no other explanation. It is definitely settled that in certain cases the bar to fertility is merely the mechanical inability of the spermatazoon to penetrate the ovum. It seems reasonable that the stimulation effect may be illustrated by borrowing Galton's polyhedron.

[6] The parent ears were, therefore, one year older, but their germination was good, and their growth equal to inbred seed of the same ages as the hybrid seed.

indication of the comparative vigor of each strain was obtained. Unfortunately crows and chipmunks played havoc with the "stand" in a number of cases, and accurate figures can not be given except in the following four cases where the stand was perfect.

A white dent no. 8 yielded 121 bushels per acre (at 70 pounds per bushel); a yellow dent no. 7, which had been inbred artificially for three years, yielded 62 bushels per acre; the cross between the two varieties, no. 7 ♀ × no. 8 ♂, yielded 142 bushels per acre.

Longfellow, no. 34, an eight-rowed, yellow flint yielding 72 bushels per acre, was crossed with the same no. 8 white dent, yielding 121 bushels per acre; the resulting cross yielded 124 bushels per acre.

Sturges's hybrid, a twelve-rowed, yellow flint with a tall, non-branching stalk partaking of the characters of dent varieties, was also crossed with no. 8 white dent. The flint parent yielded 48 bushels per acre, while the cross yielded 130 bushels per acre.

Two families of a yellow dent variety, which had each been inbred artificially for three years, were the parents of the fourth cross. No. 12, yielding 65 bushels per acre, was crossed with no. 7, yielding 62 bushels per acre. The F_1 generation yielded 202 bushels per acre. This last result is somewhat distorted, as five stalks per hill of the cross were allowed to grow while of the parents only four seeds per hill were planted. About 90 per cent. of the seeds produced mature stalks. Notwithstanding the closeness of planting to which this cross was subjected, however, casual observation was sufficient to show that it soared far beyond each parent in vigor of plant and size of ear.

In the remainder of the field every possible combination of dent, flint and sweet maize was grown, and in every case an increase in vigor over the parents was shown by the crosses. It is to be regretted that comparable yields could not be obtained in every instance, but, as a matter of fact, the differences were so apparent

to the eye that it is almost unnecessary. The figures presented do not show the average increase to be expected by a cross. The manuring was heavy, the cultivation intensive, and the yields were beyond the ordinary. But they do show that in practically every case a combination of two high-bred varieties of seed corn is more vigorous than either parent.

The importance of this fact in commercial corn growing is considerable, and is likely to increase in the future, for the following reason. The corn breeding methods in use vary as to detail, but their purpose is the same, namely, to produce high-yielding strains. The older idea was that continued selection of plus fluctuations would invariably yield results. At present, there are more adherents to the view that man can do more than isolate from the mixture of types we call a commercial variety the most perfect type that nature has produced in this variety. It is all line breeding, and as it is carried on on small plots, the tendency toward the production of an *inbred strain increases with the length of time the work is prosecuted.* Thus, unless new mutations intervene, chance of improvement is limited to the latent possibilities of the first breeding plot.

Shull[7] has already suggested that either definite recombination of previously isolated biotypes, or relaxation of selection after partial isolation and rejection of the less efficient biotypes, will be found to be the logical procedure in corn breeding.

The writer has become a convert to the first method

[7] Since this manuscript was sent to the printer the writer received from Dr. Shull, as a timely coincidence, a copy of a paper that he had read at the annual meeting of the American Breeders' Association, in January, 1909. In it he deals with a similar method of corn-breeding, namely, the actual isolation of homozygous strains by artificial inbreeding, and their recombination later. His method is more correct theoretically, but less practical than that of the writer. From this paper I inferred that his views must accord with the theory presented in this paper. Replies to my inquiries show that our ideas are strictly in harmony, although Dr. Shull had not treated the theoretical phase of the subject, having considered it as beyond the scope of his paper.

in a modified form, and suggests the following scheme. There must always be corn specialists to continue line breeding, and this method is not for the corn breeder, but the corn grower. The latter should purchase from the line breeder two strains of seed each year, and grow the F_1 generation of the cross between them.

The method requires a small isolated hybridization plot in addition to the commercial field. In this plot the two strains are planted in alternate rows. The male inflorescence is removed from one strain at flowering time and all of the seed for the commercial field selected from this crossed strain. Some hybrid combinations will be found to be more vigorous than others, but I am convinced that practically any cross within the subspecies will be profitable. Crosses between the subspecies, while more vigorous than the mean between the parents, have certain disadvantages, such as variation in the time of ripening, which make them less desirable for practical use.

BREEDING EXPERIMENTS WITH RATS

PROFESSOR T. H. MORGAN

COLUMBIA UNIVERSITY

The following experiments chiefly between the black and the roof rat were undertaken as one of a series to determine how far the Mendelian law of discontinuous inheritance applies to wild varieties and species. Most of the cases of Mendelian inheritance have been determined from domesticated forms in which the varieties seem to differ from each other in the loss of one or more characters. Until we know more about the results when wild varieties are crossed with their wild species or with other varieties, we can not safely apply Mendel's law to the process of evolution.

There are two species of house rats found in this country in addition to the common gray or Norway rat. One of these is the black rat, *Mus rattus*, that still exists in isolated communities in the north. It also infests, I believe, certain ports in the southern states and Central America.

The other, the roof rat or Alexandrian rat, is said to have been introduced from Mediterranean ports by ships. It is generally described as a variety of the black rat.[1] The roof rat is gray, it has the ticked or barred gray hair common to most wild rodents. It may, therefore, be looked upon as the original form from which the black rat has been derived. If this is the case we might expect to find that the gray color is the dominant one and the black the recessive, especially since in the domesticated species of the Norway rat, black is recessive to gray.

To my surprise I found that in the first generation the

[1] The black rats used in these experiments were obtained at Amherst, Mass., through the kindness of Mr. Clarence Birdseye. I am indebted to the Carnegie Station at the Tortugas and to Dr. Stockard and to Professor Edwin Linton for obtaining and transporting the roof rats used in these experiments.

hybrids are *black* whichever way the cross is made. Black is dominant to gray. In all I have thirty-two such individuals.[2] These black hybrids inbred have produced one litter of four black[3] and one gray. The numbers are too small to furnish conclusive data, but as far as they go they indicate that the two colors follow Mendel's law.

The roof rats are white below as is also the Norway rat, but there is a peculiar difference. In the roof rat the white hair is white to its very base, i. e., it is not ticked. In the Norway rat the ventral hair has a dark base as in most other rodents.

All attempts to cross the black rat or the roof rat with the Norway rat, or with its domesticated varieties have failed, although by putting young rats together I have had them live in harmony for a year or more. It would appear that the two species *M. decumanus* and *M. vattus* are infertile.

On the contrary as stated above *M. vattus* and *M. alexandrinus* are perfectly fertile inter se.

In respect to the ticking of the ventral hair it is interesting to note that spotted gray mice of the domesticated breeds have the hair of the white spots uncolored all the way to the base, as in the albino. I have found a wild species of brown mouse that has a white belly and the hair is ticked, i. e., it has a dark base. When such a mouse is crossed with a spotted mouse the first generation is gray with a white belly—the hair being ticked. Such mice inbred produce amongst other combinations some spotted mice. In these mice wherever a white spot extends down the sides and across the belly the region of the spot on the belly has hairs white to the base. In other words, the white spot dominates the white belly in the same way that it dominates the gray hair of the sides and back.

[2] There is some variation in the color of the black hybrids of the first generation. One that was reddish black at first later became black.

[3] In the second generation the four black individuals, still young, show some differences in the shades of black.

If the white belly of the roof rat turns out to be a character separable from the uniform gray coat, as I have found to be the case with white-bellied gray mice, we may expect to find in the second generation of hybrids some gray rats with a gray belly.

The chief point of theoretical interest in these results concerns the origin of the black color in the black rat. If it is produced by the loss of the ticking factor, as Castle suggests for other black rodents, it is inexplicable why the black should dominate when crossed with the ticked gray coat of the roof-rat. If, on the other hand, the rat has arisen by the black color spreading over and obscuring the ticking beneath, then we could understand how it dominates in the first generation; also why the result is different from that when the black variety of the Norway rat is crossed with a gray rat. It remains for further work to settle this point.

The common gray or Norway rat has, as stated, a white belly—the white hairs having a black base. When such a rat is bred to an albino having black (possibly gray also) as a latent character, the first generation contains only gray rats as Crampe and Doncaster have shown; but the color of the belly varies—a point that has hitherto escaped notice In some individuals the ventral hair is a slate-color, in others it is nearly white. In both the base of the hair is blackish. There appears to be an almost, perhaps a complete, gradation between white and slate-colored belly. The extremes may be accounted for as follows: The albino may carry black-bearing and gray-bearing germ cells. When the former unite with a gray-bearing germ cell of the gray Norway rat, the addition of black may cause the black base of the ventral hair to extend farther out towards the tip, making the belly slate-color. When a gray-bearing germ cell (of the albino) meets the gray-bearing germ cell of the albino, little or no change may take place in the ventral region.

Another interpretation is also possible. The albino may carry a uniform coat, *i. e.*, one that gives gray (or

slate) below instead of white. The presence of this condition may dominate in some of the first hybrids.

In addition to the points noted above it should be recorded that in nearly all of the individuals, resulting from a cross between a wild gray Norway rat and an albino, there occurs a pure white spot or streak on the belly, as other observers have recorded. The hair of these spots is white to its base. This result is obviously due to the incomplete dominance of the uniform coat. The albino in my experiments, carried, latent, not only black, but a spotted "condition," as the second generation demonstrated. The presence of this condition in the hybrids of the first generation is shown to the extent of the white ventral spot. This region of the body is, as it were, a "weak" area in which the recessive character displays itself, although elsewhere, as a rule, the spotting is suppressed. The result shows that at certain points in the pelage a recessive character may crop out in a dominant-recessive individual.

In the second generation gray, black, spotted gray, spotted black and albinos appear, as others have already shown. In the uniform gray individuals a series of types occur varying from rats with white bellies, like that of the wild gray rat, to those with a uniform slate-colored belly. The gray color itself is subject to some variation —the result depending perhaps on the condition of the black present.

SHORTER ARTICLES AND DISCUSSION

THE CHUB AND THE TEXAS HORN FLY

In the upper reaches of the waters of the Niobrara River, locally known as Running Water, the common chub, *Semotilus atromaculatus*, is very abundant. One may with a hook and line secure many dozens of them in a very short time. In Running Water they scarcely ever attain a greater length than eight inches. During the past summer while out on a collecting trip into the Miocene beds of northwestern Nebraska, some interesting observations were made on certain feeding habits of the chub which may prove of interest to those naturalists who are especially interested in animal behavior and intelligence.

The horn fly, *Hæmatobia serrata*, according to Kellogg, is a European insect which gets its popular name from the habit of clustering on the bases of the horns of cattle. It was first

introduced into this country about 1886 or 1887 and its spread has been so exceedingly rapid that in a very few years it has become an annoying pest to western cattle. Mr. James H. Cook, a prominent ranchman of Sioux County, Nebraska, told me that

he had never seen the horn flies so abundant as they were the past summer. They literally swarmed around the cattle and since the majority of the stock was dehorned the insects would settle all over the backs and sides of the animals although they were in some cases observed to cluster around the horn bases.

At Harris's ford, where the collecting parties crossed Running Water, several hundred cattle watered all summer. The lower part of the ford is quite shallow, scarcely attaining a depth of more than a foot; somewhat to the right the water deepened so that the cattle in drinking would be submerged nearly to the middle line of their bodies. At noon the cattle would begin to come to water and would continue coming for some hours on hot days; on cooler days they would delay their coming somewhat; and on rainy days they frequently did not come at all. The following observations were made on hot, bright days as our party was returning to camp from the morning work. Mr. Albert Thomson called my attention to the actions of the fishes and we together made the following observations repeatedly.

The cattle would almost always enter the stream at the shallow part of the ford and gradually wade up stream, drinking as they went, until they came to the deep place near the fence where the water reached well up on their bellies. The chubs seemed to be unusually numerous at the ford, and we often wondered at the great numbers of the little fishes which we could see in schools in the clear water. Their presence was soon explained. As soon as the cattle entered the stream at the shallow place in the ford the chubs would come out from their cool and shady retreats under the grasses along the sides of the bank and hasten to meet the cattle at the shallows. Often we saw as many as a dozen or more chubs following a single cow. As soon as the water came near the bellies of the animals the chubs would leap out of the water and catch the horn flies from the sides of the cattle. Often we saw them leap as much as half their length out of the water to secure a fly which was high up on the animal's side. These observations were made on several consecutive days, and on the last day but one I was so fortunate as to secure a photograph of a chub in the act of catching a fly from the side of a cow and the photograph is published herewith.

That the fishes actually learned that the dark spots on the sides of the cattle made good food, there can be no doubt. Just how they first learned it we may not know. The chubs had fur-

ther learned that the coming of the cattle meant food for them, hence they would meet the cattle in the shallows and follow them to deeper water. The act of these fishes leaping to secure flies from the sides of cattle is so unusual that it is deemed worthy of notice and it is hoped that the incident may be of service to those interested in animal behavior.

ROY L. MOODIE.

UNIVERSITY OF KANSAS.

NOTICE OF A NEW CAMEL FROM THE LOWER MIOCENE OF NEBRASKA

In the autumn of 1906, the writer found a nearly complete skeleton of a camel, in the Lower Harrison Beds, near Agate, Sioux County, Nebraska. The skeleton is finely preserved and articulated. It had apparently been washed into a heap while the muscles still held the bones together, for it is literally tied in knots. On this account it has only been partly removed from the matrix, and so a complete description is deferred.

The type (No. HC125, private collection of the writer) is an adult animal, and consists of a complete skull and jaws, a practically complete vertebral series, fore limbs and feet, pelvis, sacrum, and the greater portion of the hind limbs and feet. The latter were damaged by erosion. It is referred to the genus Oxydactylus, and the specific name of *Campestris* is proposed.

It is apparently closely related to *O. longipes*,[1] but is a much smaller and somewhat less specialized type. This seems the more natural when we remember that *O. longipes* was found in a somewhat later horizon. The skull in general contour is very similar to *O. longipes*, but exhibits some distinct features. The upper incisors are proportionally slightly larger than those of *O. longipes*, the third incisor being a little larger than the canine. The diastema separating these two teeth is relatively shorter than in the latter, and the facial portion of *O. campestris* is relatively shorter. The premaxillae are separated at the proximal extremity by an unusually large U-shaped opening, 8 mm. wide and 10 mm. long. P^2 and P^3 are slightly more robust in the present species. The limbs are long and slender, though much shorter than those of *O. longipes*. The metacarpals are entirely separate. On the sides of the proximal end

[1] *Annals of the Carnegie Museum*, Vol. II, No. 3, pp. 434–475, 1904.

of the metacarpals are small, flat, rugose bones, remnants of metacarpals II and V. When the specimen is entirely cleaned of the matrix, a more complete description will be given.

MEASUREMENTS

	O. campestris.	O. longipes.
Greatest length of skull	290 mm.	340 mm.
Length of diastema I^3 to canine	7 mm.	13 mm.
Length of diastema canine to P^1	12 mm.	14 mm.
Length of diastema P^1 to P^2	15 mm.	18 mm.
Lengtn of continuous molar-premolar series	88 mm.	102 mm.
Length of metacarpals	275 mm.	345 mm.
Length of proximal phalanx	51 mm.	66 mm.
Length of median phalanx	20 mm.	31 mm.
Breadth of metacarpals III and V	15 mm.	23 mm.

HAROLD JAMES COOK.

September 15, 1908.

NOTES AND LITERATURE

The Chondriosomes as Bearers of the Hereditary Qualities.—Meves, in a paper entitled, "Die Chondriosomen als Träger erblicher Anlagen"[1] presents a new and interesting view in regard to the bearer of the hereditary qualities. Since Hertwig, '75, reached the conclusion that fertilization consists in the union of male and female pronuclei, the nuclear theory of heredity has been criticized by many able investigators, and the new interpretation which Meves gives at this time indicates that many are still dissatisfied with the all-sufficiency of the theory, and are eagerly seeking and grasping, as it were, the first visible sign of any other substance which may serve to carry the hereditary qualities.

Meves finds in the chick embryo, between the second half of the first and the first half of the fourth day of incubation, by means of special fixing and staining reagents, a large number of independent threads, fibers, rods or granules. The shape of these structures varies in different cells and at different times in the same cell, although they are all one and the same substance. He concludes that these structures are identical with the "Cytomikrosomen" of la Valette St. George, the "Mitochondrien" of Benda and the "Chondriokonten" of Meves, and proposes to unite them under the term "Chondriosomen." He also believes that the granules of Altmann, except those produced by regents, are identical with the chondriosomes. They have been described by Benda, Meves and others in various tissue cells, plant cells and in sex cells. Benda, '03, suggested that possibly the mitochondria might play a rôle in heredity, and with this suggestion Meves agrees.

Nägeli's idioplasm hypothesis and many other similar theories have been advanced to account for heredity, but these have been criticized on the ground that they lack a material substratum, and that they are purely speculative. Meves believes that the "fantastic structure," as it was called by Sachs, has now become a reality in the chondriosomes. While Nägeli supposed the idioplasm to produce different differentiated products by

[1] *Archiv für Mikroscopische Anatomie und Entwicklungsgeschichte*, Bd. 72, 1908.

special activities on the surrounding cytoplasm, Meves believes that the differentiated parts arise by a direct metamorphosis of the chondriosomes.

Meves realizes that the nuclear substance answers fully the demands of a hereditary substance, namely, that in fertilization the two parts must be equivalent, that there must be a reduction, and that there must be an equal division in cleavage. However, he says that it has not been proved that the nuclear substance and hereditary substance are identical, or that the nuclear substance is the only hereditary substance. He then asks the question, how far do the chondriosomes satisfy conditions demanded of a hereditary substance. It is evident that the quantity of chondriosomes present in the egg cell is much greater than that brought in by the sperm. This fact, he says, presents no great difficulty, if we suppose that the specific qualities of the chondriosomes becomes expressed through the configuration of transverse sections. According to Nägeli, an over-supply of idioplasm may be thrown out from the idioplasmic system at the time of fertilization and become changed into yolk. In favor of this view Van der Stricht and his students have shown that a part of the mitochondria of the egg cell are changed into yolk granules.

There is also the possibility that the male chondriosomes, after entrance into the egg, multiply and divide. There is not an equal division of the chondriosomes in cell division, as there is of the choromatin, but they do approximate to equality of division and any difference may be made good by increased growth.

As there is a reduction of the chromatin before fertilization, Meves suggests that there may be a reduction of the chondriosomes. However, he has not seen even the slightest indication of a reduction, and until some evidence is forthcoming, such a suggestion must remain as a mere speculation. Duesberg, '07, has shown that there is a mass reduction of the chondriosomes in the two spermatocyte divisions, but in the egg this is not true, as the chondriosomes remain scattered throughout the cell, and the resulting cells are very unequal in size.

Meves suggests another way to prevent the increase in the hereditary mass, and this is as Nägeli has shown. Nägeli supposes the male and female idioplasm to unite as a mixed product. A cross section through the union of the embryonic strands shows that the idioplasm strands, in relation to the number of micellæ rows, remains unchanged. A paternal and maternal idioplasm

thread in fertilization, then, must unite end to end to form one of double length. While Meves ascribes a large part in the transportation of hereditary qualities to the chondriosomes, he does not claim that they alone, to the exclusion of the nucleus, carry these qualities. He thinks that both nucleus and cytoplasm work together, the qualities of the nucleus being carried by the chromosomes, those of the cytoplasm by the chondriosomes.

F. PAYNE.

Cultural Bed-Mutations in the Potato.—E. Heckel[1] has reared the white-flowered *Solanum maglia* from tubers received from Sutton and from Vilmoyin. The young plants resembled perfectly typical *S. maglia*. They were transplanted from the greenhouse to a fertile garden where common potatoes had been grown the year previously. The tubers obtained differed greatly from those planted and those characteristic of this species. They weighed from ten to twenty times as much. One in particular weighed 135 grams; the flesh instead of being watery and slightly bitter as it typically is, was compact and full of starch—the tuber was edible. This tuber being planted gave, the next year, five tubers from 87 to 62 grams in weight. The other tubers (of smaller size) yielded tubers of from 50 to 5 grams—the smallest having the size of the typical tubers of *S. maglia*. The author refers to the large potato obtained by him from *S. maglia* as a mutation, but suspects that its size may have been influenced by the previous growth in the same soil of the common tubers.

[1] *Ann. des Faculté des Sci. Marseille*, XVI, 1907.

The American Journal of Science

Established by Benjamin Silliman in 1818.

The Leading Scientific Journal in the United States

Devoted to the Physical and Natural Sciences, with special reference to Physics, and Chemistry on the one hand, and to Geology and Mineralogy on the other.

Editor: EDWARD S. DANA.

Associate Editors: Professor GEORGE L. GOODALE, JOHN TROWBRIDGE, W. G. FARLOW and WM. M. DAVIS of Cambridge; Professors A. E. VERRILL, HENRY S. WILLIAMS and L. V. PIRSSON, of New Haven; Professor G. F. BARKER, of Philadelphia; Professor JOSEPH S. AIMES, of Baltimore; MR. J. S. DILLER, of Washington.

Two volumes annually, in monthly numbers of about 80 pages each.

This Journal ended its first series of 50 volumes as a quarterly in 1845; its second series of 50 volumes as a two-monthly in 1870; its third series as a monthly ended December, 1895. A Fourth Series commenced in 1896.

Subscription price, $6 per year or 50 cents a number, postage prepaid in the United States; $6.25 to Canada; $6.40 to countries in the Postal Union. Back numbers at reduced prices.

☞Ten-volume Indexes, Vols. I-X, XI-XX, fourth series, price one dollar. Address

The American Journal of Science
New Haven, Conn.

Pour paraître en 1908.

LAMARCK

sa vie, son œuvre
par MARCEL LANDRIEU.

1 vol. gr. in 8° raisin d'environ 550 p. avec un portrait en héliogravure et renfermant de nombreux documente inédite.

Sera publié dans les Mémoires de la Société Zoologique de France et mis en vente également au prix de **10 fr.** Le tirage étant trés limité, prière de souscrire immédiatement en s'adressant au Secrétaire général,

28 RUE SERPENTE, PARIS.

To Zoologists and Museums

W. F. H Rosenberg

Importer of Exotic Zoological Specimens

37 Haverstock Hill London, N. W. England

Holds the largest stock in the world of specimens in all branches of Zoology.

Just published, my new price list of BIRD'S EGGS, containing over 800 species from all parts of the world. Also price lists Nos. 6, Bird Skins (over 4,300 species), and 7, Mammal Skins, Skeletons, and Spirit Specimens (over 300 species).

Any of the above price lists sent post-free on application.

Science

A weekly journal, established in 1883, devoted to the advancement of the natural and exact sciences, the official organ of the American Association for the Advancement of Science, publishing original articles and notes on the progress of the different branches of science, the proceedings of scientific societies and academies, reviews of scientific books and articles, preliminary accounts of researches and full discussion and news on all subjects concerning scientific men and scientific and educational institutions.

Annual subscription $5.00. Single numbers 15 cents.

The Popular Science Monthly

An illustrated magazine, established in 1872, devoted to the diffusion of science, publishing articles by leading authorities in all departments of pure and applied science, including the applications of science to education and society.

Annual subscription $3.00. Single copies, 30 cents.

The American Naturalist

A monthly journal, established in 1867, devoted to the biological sciences with special reference to the factors of organic evolution.

Annual subscription $4.00. Single numbers, 35 cents.

*** To new subscribers mentioning this advertisement and enclosing one dollar, SCIENCE will be sent for three months, THE AMERICAN NATURALIST for four months or THE POPULAR SCIENCE MONTHLY for six months.*

THE SCIENCE PRESS

Lancaster, Pa.

Garrison, N. Y.

Sub-Station 84, New York.

The American Naturalist

A Monthly Journal, established in 1867, Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Organic Evolution and Heredity

CONTENTS OF SEPTEMBER NUMBER

Some results of the Florissant Expedition of 1908. Professor T. D. A. COCKERELL.

Embryology of Myosurus Minimus. DR. LEROY D. SWINGLE.

Another Aspect of the Species Question. DR. J. A. ALLEN.

The Origin of the Lateral Eyes of Vertebrates Professor G. H. PARKER.

Notes and Literature: *Heredity*—Spurious Allelomorphism, Results of Some Recent Investigations, W. J. SPILLMAN. *Human Anatomy*—Pryor on Sexual and Family Variation in Centers of Ossification, C. R. B. *Plant Cytology*—Cytological Studies on Saprolegnia and Vaucheria. DR. BRADLEY M. DAVIS. *Holothurians*—Holothurioidea, Professor CHARLES L. EDWARDS. *Enteropneusta*—Recent Literature on the Enteropneusta, Professor W. E. RITTER. *Vertebrate Paleontology*—Case on Pelycosauria of North America; Barnum Brown on the Conrad Fissure and on the Ankylosauridæ. Professor S. W. WILLISTON. *Parasitology*—The Evolution of Parasitism; Trypanosomes, H. B. W.

CONTENTS OF THE OCTOBER NUMBER

The Manifestations of the Principles of Chemical Mechanics in the Living Plant. DR. F. F. BLACKMAN.

The Desiccation of Rotifers. D. D. WHITNEY.

On the Habits and the Pose of the Sauropodous Dinosaurs, especially of Diplodocus. DR. OLIVER P. HAY.

Shorter Articles and Correspondence: Juvenile Substitutes for Smoking Tobacco. Professor WILLIAM ALBERT SETCHELL.

Notes and Literature: *Heredity*—Recent Studies in Human Heredity, DR. F. A. WOODS. *Ornithology*—Riddle on the Cause of the Production of Down and Down-like Structures in the Plumages of Birds, J. A. A. *Vertebrate Paleontology*—New Fossil Mammals from Egypt, T. D. A. C.

CONTENTS OF THE NOVEMBER NUMBER

Further Studies on the Activities of Araneads. Professor THOS. H. MONTGOMERY, Jr.

Notes on the Daily Life and Food of Cambarus Bartonius Bartoni. FLOYD E. CHIDESTER.

Some Points in the Ecology of Recent Crinoids. AUSTIN HOBART CLARK.

Shorter Articles and Correspondence: Evolution without Isolation, O. F. COOK. A Note on the Silverside, JOHN TREADWELL NICHOLS.

Notes and Literature: *Botany*—The Origin of a Land Flora, Professor DOUGLASS HOUGHTON CAMPBELL. *Plant Cytology*—Apogamy in the Ferns, Dr. BRADLEY M. DAVIS. *Experimental Evolution*—Regeneration in Lumbriculus, SERGIUS MORGULIS. *The Budgett Memorial Volume*—John Samuel Budgett, President DAVID STARR JORDAN. *Animal Behavior*—Mind in Animals, Professor H. S. JENNINGS.

CONTENTS OF THE DECEMBER NUMBER

Some Physiological Aspects of Radium Rays. Professor C. STUART GAGER.

On the Origin of Structures in Plants. W. A. CANNON.

Origin and Formation of the Froth in Spittle Insects. BRAXTON H. GUILBEAU.

Shorter Articles and Correspondence: Peculiar Abnormal Teeth in a Jack Rabbit. WILLIAM A. HILTON.

Notes and Literature: *Ichthyology*—Ichthyological Notes, President DAVID STARR JORDAN. *The Inheritance of Sex in Higher Plants*—Digest of Professor C. Correns's Memoir: Professor H. E. JORDAN.

Title Page and Index to Volume XLII.

CONTENTS OF THE JANUARY NUMBER

Juvenile Kelps and the Recapitulation Theory. Professor ROBERT F. GRIGGS.

The Larva and Spat of the Canadian Oyster, Dr. J. STAFFORD.

Shorter Articles and Correspondence: Some Notes on the Traditions of the Natives of Northeastern Siberia about the Mammoth, WALDEMAR JOCHELSON. Age of Trotting Horse Sires, F. R. MARSHALL. The Occurrence of *Batrachoceps attenuatus* and *Autodax lugubris* in Southern California, WILLIAM A. HILTON.

Notes and Literature: *Experimental Evolution*—The Effect of the Environment upon Animals, Dr. FRANK E. LUTZ. *Experimental Zoology*—The Influence of the Size of the Egg and Temperature on the Growth of the Frog, SERGIUS MORGULIS. *Parasitology*—Cestodes of Birds, Professor HENRY B. WARD.

CONTENTS OF THE FEBRUARY NUMBER

Charles Darwin and the Mutation Theory. CHARLES F. COX.

Juvenile Kelps and the Recapitulation Theory. II. Professor ROBERT F. GRIGGS.

Notes and Literature: *Plant Phylogeny*—The Origin of the Archegoniates, Dr. BRADLEY M. DAVIS. *Holothurians*—Clark's The Apodous Holothurians, W. K. FISHER. *Lepidoptera*—The Blue Butterflies of the Genus Celastrina, Professor T. D. A. COCKERELL. *Vertebrate Paleontology*—The Lysorophidæ: Stegocephala; The Cotylosauria; The Oldest Known Reptile; The Age of the Gaskohle; Bison Occidentalis; Nectosaurus; Callibrachion, Dr. ROY L. MOODIE. *Parasitology*—The Sleeping Sickness Bureau, Professor HENRY B. WARD. *Exploration*—Camp-fires on Desert and Lava, Dr. ROY L. MOODIE.

Single Number 35 Cents **Yearly Subscription, $4.00**

The NATURALIST will be sent to new subscribers for four months for One Dollar

THE SCIENCE PRESS

Garrison, N. Y. **Sub-Station 84: NEW YORK** **Lancaster, Pa.**

VOL. XLIII, NO. 508 APRIL, 1909

THE AMERICAN NATURALIST

A MONTHLY JOURNAL
Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

CONTENTS

Page

I. Heredity of Hair Color in Man. GERTRUDE C. DAVENPORT and CHARLES C. DAVENPORT. 193

II. A Mechanism for Organic Correlation. Professor G. H. PARKER. 212

III. Recent Advances in the Study of Vascular Anatomy:

Vascular Anatomy and the Reproductive Structures. Professor JOHN M. COULTER. 219

The Progress of Plant Anatomy during the Last Decade. Professor EDWARD C. JEFFREY. 230

IV. Shorter Articles and Correspondence: A Note on the Degree of Accuracy of the Biometric Constants, DR. RAYMOND PEARL. Pure Strains as Artifacts of Breeding, O. F. COOK. 238

V. Notes and Literature: *Heredity*—The Nature of "Unit" Characters, DR. W. J. SPILLMAN. *Environment*—DR. FRANK E. LUTZ. *Experimental Zoology*—Hybridology and Gynandromorphism, Professor T. H. MORGAN. *Echinodermata*—Red Sea Crinoids, DR. AUSTIN HOBART CLARK. 256

THE SCIENCE PRESS

LANCASTER, PA. GARRISON, N. Y.

NEW YORK: SUB-STATION 84

The American Naturalist

MSS. intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS

Lancaster, Pa. Garrison, N. Y.

NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

Important New Scientific Books

PUBLISHED BY THE MACMILLAN COMPANY

Botany

The Origin of a Land Flora. A Theory based upon the facts of Alternation. By F. O. BOWER, Sc.D., F.R.S. With numerous illustrations.

Cloth, gilt top, xi+727 pp., illus., index, 8vo, $5.50 net.

NOTE.—A profound study in the morphology of the lowest forms of plants, with special reference to the development of their reproductive systems. The author endeavors to show that the present land flora has originated from an aquatic ancestor, and traces the methods of specialization to the land habit, and the establishment of the forms of the higher plants. A book of the highest importance not only to botanists but to biologists in general.

NEW AND STANDARD HAND-BOOKS ON AGRICULTURE, ETC.

Elements of Agriculture, Southern and Western. By W. C. WELBORN, B.S., M.S., M.P.A.

Cloth, xvi+329 pp., illus., appendix, glossary, index, 12mo, $.75 net.

NOTE.—This is a thoroughly modern treatise on farming as practiced in the Gulf States, from the point of view of the scientific agriculturist. It is adapted to school use, but is of practical service to any farmer in that part of the country. The author is vice-director of the Texas Experiment Station.

Re-issues of the highly valued Hand-Books known as the Garden Craft and Rural Science Series, edited by L. H. BAILEY, of Cornell University, Editor of "Cyclopedia of American Horticulture," "Cyclopedia of American Agriculture," etc.

The Principles of Fruit Growing. By L. H. BAILEY.
Tenth Edition, $1.50 net, by mail $1.66.

Irrigation and Drainage. By F. H. KING.
Fifth Edition, $1.50 net, by mail $1.68.

Principles of Vegetable Gardening. By L. H. BAILEY.
Sixth Edition, $1.50 net, by mail $1.68.

Bush Fruits. By FRED W. CARD.
Fourth Edition, $1.50 net, by mail $1.66.

Fertilizers. By EDWARD B. VOORHEES.
Tenth Edition, $1.25 net, by mail $1.38

Farm Poultry. By GEO. C. WATSON.
Sixth Edition, $1.25 net, by mail $1.42

Published By **The Macmillan Company** 64-66 5th Ave., New York

THE
AMERICAN NATURALIST

VOL. XLIII *April, 1909* No. 508

HEREDITY OF HAIR COLOR IN MAN

GERTRUDE C. DAVENPORT AND CHARLES B. DAVENPORT

STATION FOR EXPERIMENTAL EVOLUTION, CARNEGIE INSTITUTION OF WASHINGTON

INTRODUCTION

Types of Hair Color.—The heredity of hair color in mammals is a subject of great complexity, not to be lightly entered upon. It is a subject in which much knowledge has been gained in recent years through the work of Bateson and his associates, Castle and his pupils, Cuenot and others. Nevertheless certain important points remain uncertain. First, and fundamental for our purpose, is the question of the number of factors involved in any hair color. All are agreed that there is a special red pigment (a lipochrome) that stains the hair diffusely. In clear red hair one sees, in sections, a yellowish red tinge that is not bound up with any structures. With a high power one sees elongated, spindle-shaped bodies, which are apparently the remains of nuclei and are devoid of granules. In all other hair (except that of albinos) one sees granules grouped in the spindle-shaped bodies. In black hair (Chinaman, Fig. A) these granules are large and numerous in each group (average, 12) and appear of a dark brown color. In very dark brown hair (negro, Fig. B) the granules are perhaps a little larger but much less numerous in each group (average, 6); and the color is a much less intense brown. In hair of a cold, mouse brown (Fig. C) (about No. 25 in

E. Fischers's hair scale[1]) the granules are small, very few in each group (average 4) and slightly colored. The dark red hair of the orangutan is due chiefly to granules whose color is well reproduced by sepia on a clear background; but in the head hair of the golden babboon, which is striped golden and black, much diffuse golden pigment is found and (in the black zones) dark sepia granules of

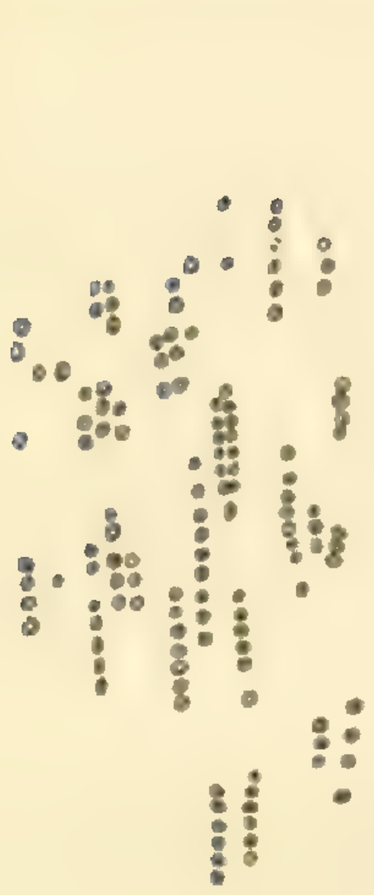


FIG. A. × 1150.
CHINAMAN.

FIG. B. × 1150.
LEON M. (NEGRO).

FIG. C. × 1150.
MOUSE-BROWN. "A."

medium size and frequency. In twoscore preparations of the hair of man and primates we have not found in any instance jet-black granules such as are characteristic of black mice. In our preparations, many of which are thin sections kindly cut for us by Miss Lutz, the granules vary in size, number and intensity, but there is no discontinuity between the lighter and darker sepia pigments; and, as stated, we have not found a coal black hair either in Chinese, Japanese, Indian, Negro or Italian, and not even in the black spider monkey. There is an interesting parallel case in poultry where even in the Black Minorcas and the Black Cochin the pigment is a dense sepia brown. We conclude, therefore, that such discontinuous color types as are described in domesticated animals such as

[1] Made by Franz Rosset, Freiburg i/Br. See E. Fischer, *Korrespondenz. Blatt, Deutsch. Gesell. f. Anthropologie, Ethnologie u. Urgeschichte,* XXXVIII, 141–147. September–December, 1907.

fancy mice and guinea pigs under the names of yellow, chocolate and black are not fundamentally distinct, but have probably been made so in the process of perfecting the standard groups. Indeed, a casual acquaintance with the variety of human hair color as one meets with it in the streets of any large city shows that there are all intergrades between yellow, light brown, dark brown and black hair and even the reds pass (through dark red and red brown) into the warm browns. It may consequently be concluded, at least provisionally, that there are two main types of pigment in human hair; a reddish yellow, which finds its intensest development in bright red, and a sepia brown whose intensity varies from a light yellow to dark brown and black. Finally, the two pigments may be combined[2] and in such cases the brown pigment may quite obscure the red.

The conclusion here reached concerning the factors involved in human hair color are not, we fear, in accord with the recent investigations on other mammals. They rather speak against the theory of well-developed unit characters in human hair pigment. Brown and black colors there are and an intensifier or a diluter; on the other hand, these are not well defined units but occur in all conceivable degrees. The facts of intensity in human hair color indicate that the absence of selection made on the basis of intensity has resulted in the blending of color unit characters or has not afforded the selective means by which they have elsewhere been formed.

General Scheme of the Tables.—The data concerning a single family are placed in one line. At the extreme left are given certain reference letters by which the family is designated. Then follow the number of children in the designated family that have hair of the class named at the top of each column. The following six columns give the color of the hair of the mother (M), father (F), mother's mother (MM), mother's father (MF), father's mother (FM) and father's father (FF) so far as known.

[2] It is clearly seen in the hair of the mother of the *Lyn* family (Table X, *b*).

The principal abbreviations of the names of hair colors are as follows: *br*, brown; *chest*, chestnut; *dk*, dark; *fl* or *flax*, flaxen; *gold*, golden; *lt*, light; *med*, medium; *n*, black; *v*, very; *yell*, yellow. Names of colors in parentheses ( ) indicate juvenile condition.

Classification of the Tables.—Three series of tables may be considered. A, including cases where black or brown pigment is absent from both parents; B, including cases when brown is present in both parents and red is not visible in either; and C, including cases where both brown and red are visible in the parentage.

A. Heredity in Absence of Black or Brown Pigment in Parentage

TABLE I. DISTRIBUTION OF HAIR COLOR IN OFFSPRING WHEN NEITHER PARENT SHOWS BROWN PIGMENT

Reference Letters.	Offspring. Tow.	Yell.	Gold.	Red.	Ancestry. M.	F.	MM.	MF.	FM.	FF.
Rit	4				flax	flax	flax	flax	flax	flax
Hak	11	2			lt. yell.	flax	"lt."	"lt."	"lt."	flax
Dex	1	4			blond	blond	blond	blond	blond	blond
Ste-E	2				gold	flax	br.	br.	lt. br.	N(flax)
Reg-A			6		gold	gold	gold	gold	gold	gold
Edw				3	dk. red	lt. red	—	—	—	—
Swe	2		1		lt. red	flax	lt. br.	dk. br.	dk. br.	dk. br.

B. Heredity of Black and Brown Pigment in Parentage

TABLE II. DISTRIBUTION OF HAIR COLOR IN OFFSPRING OF PARENTS ONE OF WHOM HAS THE LEAST INTENSITY OF BROWN (FLAXEN, GOLDEN) AND THE OTHER A SLIGHTLY GREATER INTENSITY OF BROWN (LT. BR.)

Reference Letters.	Offspring. Flax.	Yell.	Yell.-Br.	Lt. Br.	Red.	Ancestry. M.	F.	MM.	MF.	FM.	FF.
Boy-A	2					flax	lt. br.	lt. br.	blond	lt. br.	lt. br.
Hal-A		1		2	1	lt. br.	flax	N.	lt. br.	flax	flax
Deg			1	1		lt. yell.	lt. br.	br.	dk. br.	lt. br.	lt. br.

The foregoing 7 families, comprising 36 children, illustrate a simple case. When both parents lack the brown pigment the children will all lack it. When the diffuse

pigment has a weak intensity in the parents it will have the same character in the children; but where it has a strong intensity, as red, in the parents it may have the strong intensity in some (Swe) or all (Edw) of the children.

As compared with Table I, Table II shows a greater variation in the offspring—the classes light brown and yellow brown make their appearance and comprise just 50 per cent. of the offspring, a result that accords with the hypothesis that light brown is heterozygous and flaxen or light yellow is recessive, for, DR × RR is expected to yield 50 per cent. of the DR (light brown) type. We note here as in Table I that the hair is in no case darker in the children than in the darker parent; but it may be less dark.

TABLE III. DISTRIBUTION OF HAIR COLOR IN THE OFFSPRING WHEN BOTH PARENTS HAVE LIGHT BROWN HAIR

Reference Letters.	Offspring.					Ancestry.					
	Flax.	Gold.	Yell.-Br.	Lt. Br.	Auburn.	M.	F.	MM.	MF.	FM.	FF.
Byr		3	1		2?	lt. br.	lt. br.	dk. br.	N.	lt. br.	br.
Klo	2	1		1		lt. br. (fl.)	lt. br. (fl.)	lt. br. (fl.)	N.	"lt."	br.
Pla-B				6		lt. br.	lt. br.	lt. br.	lt. br.	N.	N.
Ste-G				2		lt. br.	lt. br.	br.	lt. br.	br.	—
Tuc				2		lt. br.	lt. br.	lt. br.	N.	dk. br.	gold
Totals	2	4	1	11	2?						

Assuming two cases of "auburn brown" in Byr family to be essentially golden brown (this hair has not been seen by us) it appears that when both parents have light brown hair either all of the children are of the same type (Pla-B, Ste-G, Tuc. families) or else of the light brown and lighter (yellow brown to flaxen—Byr?, Klo. family). In the first case the parents act like homozygous dominants toward the lighter types; in the second case like heterozygous dominants.

In this case we obtain a total of 42 offspring, 16, or 38 per cent., dark brown and brown, and 26, or 62 per cent., light brown or lighter. Taking dark brown as hetero-

TABLE IV. DISTRIBUTION OF HAIR COLOR IN THE OFFSPRING WHEN ONE PARENT HAS DARK BROWN HAIR AND THE OTHER LIGHT BROWN

(*a*) *The Darker Parent Produces "Light" Germ Cells as well as "Dark."*

Reference Letters.	Offspring.								Ancestry.					
	Flax.	Yell.	Yell.-Br.	Gold.	Lt. Br.	Br.	Dk. Br.	N.	M.	F.	MM.	MF.	FM.	FF.
Bri					4		1		dk.br.	lt.br.	lt.br.	dk.br.	dk. br.	flax
Dou-A				1	2	2	1	1	dk.br.	lt.br.	lt.br.	dk.br.	dk. br.	lt. br.
Dou-B			1				3		lt.br.	dk.br.	dk.br.	lt.yell.br.	dk.red	N.
Fir		1			3				lt.br.	dk.br.	br.	br.	br.	dk.br.
Loc-B			2						dk.br.	lt.br.	yell.-br.	dk.br.	lt.br.	yell.-br.
Loe					4				dk.br.	lt.br.	lt.br.	N.	dk.br.	dk.br.
Mat-B					2				lt.br.	dk.br.	br.	dk.br.	lt.br.	dk.br.
Mor-A					2				dk.br.	lt.br.	lt.br.	dk.br.	dk.br.	N.
Ran-B					3	3	3		dk.br.	lt.br.	lt.br.	br.	br.	lt.br.
Sho					1		2		dk.br.	lt.br.	lt.br.	lt.red	dk.br.	br.
Totals	1	3	1	21	5	10	1							
	26				16									

zygous and dominant to light, expectation is 50 per cent. of the offspring as dark as or somewhat less dark than the darker parent and 50 per cent. light. The observed frequencies are of the expected order.

(*b*) *The Darker Parent is not Known to be Heterozygous in Hair Pigment.*

Reference Letters.	Offspring.					Ancestry.					
	Flax.	Gold.	Lt. Br.	Br.	Dk. Br.	M.	F.	MM.	MF.	FM.	FF.
Bin			1	2		dk. br.	lt. br.	dk.br.	N.	br.	dk. br.
Fis			3		1	dk. br.	lt. br.	dk.br.	dk.br.	lt. br.	lt. br.
Fri			2		1	dk. br.	lt. br.	br.	N.	br.	blond
Gil-B	1		2		1	dk. br.	lt. br.	dk.br.	dk.br.	lt. br.	lt. br.
Gue	2			2	1	lt. br.	dk.br.	dk.br.	N.	dk. br.	N.
Hal-E			1	2	2	dk. br.	lt. br.	br.	br.	N.	lt. br.
Huf	1		2			lt. br.	dr. br.	lt. br.	dk. br.	dk. br.	dk. br.
Lat-A		2	2		1	v. dk.br.	lt. br.	N.	N.	N.	N.
Pot			2		2	dk. br.	lt. br.	dk. br.	dr. br.	dk. br.	dk. br.
Rog-B			3		1	dk. br.	lt. br.	dk. br.	dk. br.	N.	lt. br.
Sin					2	lt. br.	dk.br.	lt. br.	—	"dark"	dk. br.
Sne			2			lt. br.	dk.br.	lt. br.	dk. br.	dk. br.	N.
Wil-D		1	1	2	2	lt. br.	dk.br.	lt. br.	lt. br.	dk. br.	N.
Totals	4	3	21	8	14						
	28			22							

In this case we obtain in a total of 50 offspring, 22, or 44 per cent., dark brown and brown and 28, or 56 per cent.,

light brown or lighter. Were the dark brown parents truly homozygous in hair color, and did the hair color of the offspring not grow darker with age, Mendelian expectation would be 100 per cent. dark brown. Actually, the result falls far short of that, just as the necessary conditions are far from being met. It is highly probable that in some of these families (notably Gil-B, Gue and Huf, and probably also Lat-A and Wil-D) the darker parent actually forms germ cells that lack black pigment. Of the four lightest haired children the ages of three that are known are 8, 10 and 15 years—ages at which the adult color is not fully shown. Under these circumstances one can not predict with certainty the outcome of matings of this class. One can only say that the proportions of light brown children and those with lighter hair should be less in proportion to the darker haired children in class B than in class A. The actual proportions in the two classes are in the direction of this expectation.

TABLE V. DISTRIBUTION OF HAIR COLOR IN THE OFFSPRING WHEN ONE PARENT HAS BLACK HAIR AND THE OTHER LIGHT BROWN HAIR
(NO DIVISION, ON ACCOUNT OF FEWNESS OF FAMILIES)

Reference Letters.	Offspring.							Ancestry.					
	Flax.	Yell. Br.	Gold.	Lt. Br.	Br.	Dk. Br.	N.	M.	F.	MM.	MF.	FM.	FF.
Car-B				1	3		1	N.	lt. br.	br.	N.	lt. br.	lt. br.
Dey				3				N.	lt. br.	dk. br.	N.	br.	N.
Dra		1		1				N.	lt. br.	dk. br.	N.	dk. br.	dk. br.
Jem				2		1		N.	lt. br.	lt. br.	N.	dk. br.	lt. br.
Ski		1		2		2		lt. br.	N.	"fair"	br.	N.	N.
Ser						2		N.	lt. br.	dk. br.	"light"	lt. br.	N.
Spr			1	1	1	1		lt. br.	N.	—	—	—	—
Str-B	2	1		3				lt. br.	N.	N.	lt. br.	lt. br.	—
Tre				2	1			N.	lt. br.	N.	dk. br.	—	—
Totals	2	3	1	15	5	6	1						
				21									
						12							

Assuming what is probably true for all the families, that the black-haired parent produces an equal number of germ cells with a tendency toward lighter hair and toward black, we should expect an approach toward an equality

of light and dark haired offspring. Actually, the lighter colors are in excess—a result again doubtless due to the

TABLE VI. DISTRIBUTION OF HAIR COLOR IN THE OFFSPRING WHEN ONE PARENT HAS BLACK HAIR AND THE OTHER BROWN HAIR

Reference Letters.	Offspring.						Ancestry.					
	Flax.	Gold.	Lt. Br.	Br.	Dk. Br.	N.	M.	F.	MM.	MF.	FM.	FF.
Blo-A			3	2			N.	br.	—	—	—	—
Cas		1	1				N.	br.	br.	N.	flax	N.
Clu-A				3			br.	N.	—	—	—	—
Clu-B			1	1		1	br.	N.	—	—	—	—
Col-C	1		1	2	1		br.	N.	lt. br.	N.	dk. br.	lt. br.
Dru-B			3				N.	br.	—	—	—	—
Hen			1	1	1		br.	N.	N.	br.	N.	yell.-br.
Hof		1	2				br.	N.	lt. br.	lt. br.	N.	N.
Koo		1		1			br.	N.	br.	br.	br.	br.
Lea			1	2			br.	N.	br.	br.	br.	br.
Mil-A			1	1	1		N.	br.	br.	N.	N.	br.
Ros			3	2			N.	br.	br.	br.	br.	N.
Sea				4			br.	N.	br.	br.	br.	N.
Ste-D						7	br.	N.	N.	—	—	—
Sto-B					1	1	br.	N.	br.	dk. br.	br.	N.
Ver		1			1		N.	br.	br.	lt. br.	dk. br.	N.
Totals	1	4	17	19	5	9						
	22			33								

relative immaturity of the children as compared with their parents.

Assuming, as in the discussion of Table V, that the blacks are heterozygous (except in the Ste-D family) we should expect an equality of dark and light haired offspring modified by preponderance of the lighter type owing to the immaturity of the average of the offspring. Actually, with brown hair and lighter there are 41 children as opposed to 7 (Ste-D omitted) kith either black or dark brown hair. When we compare the proportion of the children having hair brown or darker in this Table (60 per cent.), with that in Table V (36 per cent.) we realize how much more frequent the darker classes have become with the increased darkness in the hair of the second parent.

On account of the impossibility of drawing the line between the dark and the light shades of hair and on account

of the light color of immature offspring we are able only to compare this section with that which follows.

TABLE VII. DISTRIBUTION OF HAIR COLOR IN THE OFFSPRING WHEN BOTH PARENTS HAVE DARK BROWN OR BLACK HAIR

(a) When Both Parents Probably Form Light Germ Cells and Dark in Equal Numbers

Reference Letters.	Offspring.								Ancestry.					
	Yell.	Yell.-Br.	Gold.	Lt. Br.	Br.	Dk. Br.	N.	Chest.-Br.	M.	F.	MM.	MF.	FM.	FF.
Cam-A	1			4	3		2		N.	N.	"med."	N.	lt.br.	N.
Can				2					N.	N.	dk.br.	N.	dk.br.	lt.br.
Cla-A				1		3			dk.br.	dk.br.	lt.br.	dk.br.	lt.br.	lt.br.
Cur				1		1			dk.br.	dk.br.	lt.br.	br.	lt.br.	dk.br.
Fue	1	1				1			dk.br.	dk.br.	blond	dk.br.	dk.br.	blond
Gla-B	1	1		2		2	1		N.	N.	yell.-br.	N.	N.	br.
Gor-A			2	3		2	4		dk.br.	N.	N.	br.	N.	br.
Had				2	1				dk.br.	N.	N.	lt.br.	br.	N.
Har-A		1		3		3	2		dk.br.	N.	br.	br.	br.	br.
Hem-A				1	1	1			br.	N.	N.	br.	N.	yell.-br.
Mck						1		1	N.	N.	br.	br.	N.	br.
Rol				1		4	1		N.	dk.br.	br.	N.	lt.br.	dk.br.
Sim			1			1			N.	N.	N.	lt.br.	lt.br.	lt.br.
Totals	3	3	3	20	5	19	10	1						
	29				35									

Assuming that the qualities of light hair color and dark hair color (or absence and presence of intensifier) segregate in parents of mixed origin expectation is that Series A would yield 75 per cent. dark haired offspring, but on account of the impossibility of drawing the line between the dark and light shades of hair and on account of the light color of immature offspring we are able only to compare this series with series *b* in which expectation is 100 per cent. offspring of the darker color. Actually, in series *b* there are 59 individuals light to 137 (or about 70 per cent.) dark while in series *a* only 55 per cent. are dark. A part of these light haired individuals probably result from recessive light hair color of parents and a part from immaturity.

(b) When Both Parents are not Known to Form Light Germ Cells

Reference Letters.	Offspring.								Ancestry.					
	Flax. Yell.	Yell.-Br.	Gold.	Lt. Br.	Br.	Dk. Br.	N.	Chest. Red.	M.	F.	MM.	MF.	FM.	FF.
Bal				3		3			dk.br.	dk.br.	dk.br.	dk.br.	dk.br.	N.
Bar-A				4		2			dk.br.	dk.br.	N.	N.	dk.br.	N.
Bec-A				1	1	1	1		dk.br.	N.	lt.br.	N.	N.	N.
Bra-C				1		1			dk.br.	dk.br.	N.	lt.br.	—	dk.br.
Bra-D					1	3	2		N.	N.	dk.br.	N.	N.	dk.br.
But		1				2	1		dk.br.	N.	N.	N.	N.	dk.br.
Can				2					N.	N.	dk.br.	N.	dk.br.	lt.br.
Cap				1		3			N.	N.	N.	N.	N.	—
Cla-C						2			N.	dk.br.	br.	N.	lt.br.	lt.br.
Cla-D				2		3			dk.br.	dk.br.	br.	dk.br.	br.	dk.br.
Dav-B				2	1	1			dk.br.	N.	N.	N.	N.	N.
Dor-B				2		2	3		N.	N.	br.	N.	N.	N.
Fal			1	2	1	2	1		dk.br.	dk.br.	N.	N.	N.	yell.-br.
Fie	2			1	1	1			dk.br.	N.	br.	dk.br.	dk.br.	br.
Gar	[1][1]			[1][2]			3		N.	N.	N.	N.	N.	N.
Gra-A	1			1	1	1			dk.br.	dk.br.	N.	N.	yell.-br.	N.
Gre-A						2			N.	dk.br.	N.	N.	dk.br.	dk.br.
Gro-A					1	2			dk.br	dk.br.	dk.br.	dk.br.	dk.br.	dk.br.
Hed				1	2	1	1		dk.br.	dk.br.	br.	N.	N.	br.
Hew-A				1[3]		2	2		N.	N.	N.	N.	N.	N.
Hit				1		1			dk.br.	N.	N.	N.	dk.br.	dk.br.
How-B	1			3		2			dk.br.	N.	dk.br.	N.	—	N.
Keh						4	1		N.	N.	N.	N.	N.	N.
Lay				3	2				dk.br.	dk.br.	br.	br.	dk.br.	dk.br.
Leo				1	1	1			N.	dk.br.	gold	N.	N.	dk.br.
Lit-B				1	2				dk.br.	dk.br.	dk.br.	dk.br.	br.	lt.br.
Los				1		2	1		N.	N.	N.	N.	br.	yell.-br.
Mag				2		4			dk.br.	N.	dk.br.	N.	N.	dk.br.
Meb					1	3	1		N.	N.	—	—	N.	—
Nor	3					3			dk.br.	dk.br.	dk.br.	N.	N.	flax
Oke				1	1		1	1	dk.br.	N.	br.	N.	N.	N.
Par-B					1	2			N.	dk.br.	br.	N.	N.	N.
Poe		1			2				dk.br.	N.	N.	yell.-br.	N.	N.
Put				2		4			dk.br.	dk.br.	dk.br.	dk.br.	lt.br.	N.
Ram					1		1	1	N.	N.	N.	N.	N.	N.
Rem	1				1				dk.br.	dk.br.	dk.br.	dk.br.	dk.br.	dk.br.
Ric-C				1		1	1	2	N.	N.	N.	N.	N.	N.
Rob-B					2	1	2		N.	dk.br.	br.	N.	br.	dk.br.
Sam-B		2		1		2			dk.br.	dk.br.	N.	N.	N.	N.
Sel				1		1	2		dk.br.	N.	dk.br.	N.	N.	N.
Squ				1		1	3		N.	N.	N.	N.	N.	N.
Sto-C						2			N.	N.	N.	N.	dk.br.	N.
Tho-D				1	1		1		dk.br.	N.	dk.br.	N.	dk.br.	N.
Tru	1					2			dk.br.	dk.br.	dk.br.	yell.-br.	dk.br.	dk.br.
Was					1	2	2		dk.br.	dk.br.	N.	N.	dk.br.	dk.br.
Whe-A					5		1		N.	N.	N.	dk.br.	—	—
Wol	1[4]								N.	N.	N.	N.	N.	N.
Totals	8 2 4 1 44					30 72 31 1 3								
	59					137								

[1] 9 years old. [2] 6 years old. [3] Also 3 flaxen, 5 to 10 years old. [4] Also 3 "blond," 1–9 years old.

C. Heredity of Red and Brown Pigment

We have seen that the red series is quite independent of the yellow-brown series. Clear red-haired individuals lack black pigment themselves and can not transmit it to their offspring. This is, at least, *a priori* probable; but despite careful search we have found no case of two parents with clear red hair. One case of clear red and dark red is given in Table I., Edw family, in which all three children have red hair. We have one of dark red × dark red parentage with the following remarkable record (as yet unchecked).

Reference Letters.	Offspring.				Ancestry.					
	Yell.	Gold.	Brown.	Black.	M.	F.	MM.	MF.	FM.	FF.
Dey-B	1	3	1	4	dk. red	dk. red.	—	N	br.	N

We interpret this case to mean that the red is absent in some children (owing to heterozygotism of the parents) and dilute in others and here masked by black pigment.

Table VIII. Distribution of Hair Color in the Offspring when One Parent has Hair of a Clear Red Color; the Other of a Brown

Reference Letters.	Offspring.								Ancestry.					
	Flax.	Yell. Br.	Lt. Br.	Br.	Dk. Br.	N.	Chest.	Lt. Red	M.	F.	MM.	MF.	FM.	FF.
Bon								4	br.	lt. red	N.	br.	br.	br.
Bow		1	2		1		1		red	br.	N.	N.	—	br.
Dig			4			1			N.	red	—	—	—	—
Hur	1		3						lt. red	lt. br.	lt. br.	dk. br.	lt. br.	dk. br.
May	[1]		1				1		lt. red	br.	lt. red	flax	yell. br.	dk. br.
Web		1	1	1		2		2	lt. red	N.	lt. red	N.	N.	N.
Totals	1	2	11	1	1	3	2	6						

In this table the yellow-brown series of colors predominates among the offspring over the reds. This we interpret to mean that, as the red parents are usually heterozygous in the intensity of red that they bear, we have approximately one half of the offspring without any (or only a slight) tendency toward red. Even when red

dominates over its absence it is frequently completely hidden by black or even dark brown. In consequence of the cooperation of these two causes we are not surprised to find considerably more than half of the offspring (70 per cent.) *showing* no red.

TABLE IX. DISTRIBUTION OF HAIR COLOR IN THE OFFSPRING WHEN THE PARENTS HAVE DARK HAIR CONTAINING HYPOSTATIC RED.

(a) Both Parents Have Hypostatic Red

Reference Letters.	Offspring. Flax.	Yell.	Yell. Br.	Gold.	Lt. Br.	Br.	Dr. Br.	N	Chest.	Lt. Red.	Ancestry. M.	F.	MM.	MF.	FM.	FF.
Far					1					1	dk.br.	dk.br.	dk.br.	lt. red	dk.br.	red
Hog-B					1		1		1		dk.br.	dk.br.	chest.	N.	chest.	—
Kel					1					2	N.	N.	—	—	—	—
Smi-D							1		3		dk.br.	N.	N.	chest.	chest.	chest.
Totals					2	1	2	0	4	3						

(b) Only One Parent is Known to Have Hypostatic Red.

Beo-A					2	1	2	5			N.	N.	br.	chest.	br.	N.
Dev					1		1				dk.br.	N.	lt.br.	N.	—	red
Gla-A						3	3	2			N.	dk.br.	N.	chest.	dk.br.	N.
Got		1		1			1	1			N.	N.	N.	N.	N.	red
Pat-A			1		1	4	3	1			N.	N.	red	dk.br.	N.	N.
Wan-A					1	1	1				N.	dk.br.	dk.br.	dk. red	br.	dk.br.
Wel-A	2					2	5	1			N.	dk.br.	N.	dk. red	—	dk.br.
Whe-D						1		1			N.	N.	dk. red	N.	lt.br.	N.
Woo-B							2				N.	dk.br.	dk.br.	gold	chest.	gold
Totals	2	1	1	1	5	12	18	11								

Tables VIII to X give data for answering the very difficult question of inheritance of red when associated with melanic pigment. The chief difficulty is due to the masking of the diffuse by the more intense granular pigment. The following results seem, despite this difficulty, established.

1. Two light-haired parents whose hair is without red will have no red-haired children (Table I).

2. When one parent only forms "red hair" gametes, while the other forms exclusively gametes containing the darker phases of melanic pigmentation, the offspring will show no red hair; *a fortiori*, if neither parent forms "red hair" gametes, no red hair will appear in the offspring. (Table IX, *b*; compare also Tables IV, V, VI and VII.)

TABLE X. DISTRIBUTION OF HAIR COLOR IN FAMILIES CONTAINING RED-HAIRED CHILDREN; AND THE HAIR COLOR OF THE ANCESTORS OF THESE FAMILIES

Reference Letters.	OFFSPRING.										ANCESTRY.					
	Flax.	Yell.	Yell.-Br.	Gold.	Lt. Br.	Br.	Dk. Br.	N.	Chest.	Lt. Red.	Dk. Red.	M.	F.	MM.	MF.	FM.	FF.
(a) Both Parents Have Red Visible in Hair																	
Edw										2	1	dk.red	lt.red	—	—	—	—
(b) Only One Parent Has Red Visible in Hair																	
Bur-B						3				1		auburn	dk.br.	auburn	auburn	dk.br.	dk.br.
Bow										4		br.	br.-red	N.	br.	br.	br.
Fin				1						1		dk.br.	dk.red	dk.br.	dk.br.	lt.br.	dk.br.
Hol-D							1			1		red	dk.br.	dk.br.	br.	N.	br.
Lyn				2						1	1	red.-br.	br.	chest.	br.	br.	br.
Mur		1			1						1	dk.red	lt.br.	dk.red	N.	dk.br.	dk.br.
Mye					1	1				2		br.	dk.red	red	br.	N.	br.
Pad					1						4	lt.br.	dk.red	N.	N.	—	—
Rav					1					1		dk.red	dk.br.	dk.red	—	—	—
Wri										3		dk.br.	sandy	dk.br.	br.	sandy	br.
Web		1			1	1		2		2		dk.red	N.	N.	br.-red	N.	N.
Totals		2	3	5	5	1	2	0	16	6							
					18				22								
(c) Neither Parent has Red Visible in Hair																	
Bol			1	1					1	1		yell.-br.	N.	lt.br.	dk.br.	—	—
Ear						1				1		dk.br.	dk.br.	v.dk.br.	br.-red	dk.br.	red
Elt					2					1		br.	lt.br.	dk.br.	lt.br.	lt.br.	br.
Fan						1		2		2		br.	N.	N.	N.	N.	N.
Fra-D											2	N.	N.	—	—	—	—
Fri-B					2	2					1?	lt.br.	lt.br.	br.	lt.br.	lt.br.	—
Fro					1	1	1			1		lt.br.	br.	br.	lt.br.	—	—
Gri			1		1		2	1	1		1	N.	br.	yell.	dk.br.	red	N.
Had-A											2	N.	br.	N.	N.	N.	br.
Kel					1					2		N.	N.	—	—	—	—
Mcg-B					1	3				3		N.	br.				
Pra		1		3			2	1		1		yell.-br.	dk br.	gold	N.	N.	dk.br.
Ram						1		1			1	N.	N.	N.	N.	N.	N.
Ric					1		1	1		2		N.	N.	N.	N.	N.	N.
Sco		2	1				1			1	1	lt.br.	N.	br.	N.	red	N.
Tay					1		1				1	lt.br.	dk.br.	br.	br.	br.	dk.br.
Wal-C						2	1			3	2	br.	N.	N.	dk.br.	dk.br.	N.
Wri-A					3		1	1		2		dk.br.	N.	dk.br.	N.	red	br.
Totals	1	4	5	13	13	9	6	2	20	11							
				51					33								

3. When, on the other hand, both parents, though very dark, produce "red hair" gametes, about three sixteenths of the offspring will have clear red hair. (Table IX, *a*: the ratio is 3 in 12.)

4. Conversely red-haired children result from the union of two "red hair" gametes. If there is no black pigment to be considered all children, in such cases, will have red hair. If one parent has visible red and the other none (though probably heterozygous) then about half of the children show the lipochrome pigment and the other half the melanic pigment (Table X, *b*). If neither parent of red-haired children shows red in its (dark) hair then expectation is that only three sixteenths of the offspring will have red hair. Table X, *c*, shows only those families in which red actually occurs. Now in some families with the potentiality of red in one quarter of the offspring, but having only four or fewer children, a red-haired child may fail to occur and such a family would be excluded from the table. Such an exclusion would tend to reduce the proportion of non-red offspring in the total. Consequently instead of 86 per cent. of the offspring in Table X, *c*, being non-red, actually only 61 per cent. are such. In the families given there are numerous cases where the red haired are to the non-red haired offspring as 3 is to 13 or as nearly so as the size of the family permits. This is true of the Bal, Elt, Fro, Gri, Ram, Sco and Tay families. The other families show not unreasonable divergencies from the typical 3 to 13.

5. All results are in accord with the statement that red and black constitute two independent series; that red is dominant over no red, as the deeper shades of melanic pigment are dominant over the lighter; and that the dense granular melanic pigment tends to hide the diffuse pigment. Thus in Table VIII the gametes of the red-haired parent may be given as n.R; those of the brown-haired parent as N.r; where N, n. are abundance and sparsity of melanic pigment, respectively, and R, r presence and absence of lipochrome (red) pigment, respectively. Then the zygotes will be of the various forms: nR (red soma), NR (brown or black, red hypostatic), Nr (plain brown or black), n.r. (flaxen to light brown). The matings of Table IX, *a*, are of the order (NR, Nr, nR, nr) × (NR,

Nr, nR, nn). Expectation in 12 offspring is 6.7 dark brown or chestnut, 2.3 clear red, 2.3 pure brown or black and .7 very light brown. This expectation is approximately realized in the totals. The matings of Table IX, *b*, are of the order (NR, Nr, nR, nr) × (Nr). There is actually a total of 51 individuals and expectation in this case is 25.5 offspring with deep melanic or chestnut hair and 25.5 offspring with pure melanic pigmentation of some grade. No pure red should appear and none does occur. The matings of Table X, *b*, are of the order (NR, nR) × (nR). They should give an equality of offspring of the two types: NnRR (melanic pigmentation with hypostatic red) and nnRR (red with little or no black). The matings of Table X, *c*, are of the order (NR, nR, Nr, nr) × (NR, nR, Nr, nr). This should yield in a total of 73 offspring 43.9 having dark melanic pigment combined with (hypostatic) red; 14.6 with pure brown of some grade; 14.6 with pure red and 4.9 with sparse melanic pigmentation (yellow brown). The important proportional excess of the reds is explained in the last paragraph.

D. Is Inheritance of Hair Color at all Blending and can it be said to conform to Galton's Law?

We have seen that, despite the difficulties offered by change of hair color with age and by the masking of diffuse red pigment with brown granular pigment, inheritance in hair color can be brought into accord with the ordinary formula for alternative inheritance. But it may fairly be asked, since brown pigment is not a well-defined unit character, whether hair color may not equally conform to the blending type of inheritance. If there were blending ("as in human skin color"?) then the offspring of a dark and light should all be intermediate. Table V is important in this inquiry. If blending occurred the offspring of black and light brown should all be brown (or light brown because of immaturity) but dark browns and a black occur; so in Table VI the 9 blacks oppose the hypothesis; also in Tables VIII and

IX, *a*, the occurrence of red is not in accord with the hypothesis. Certainly there is no blending in an "all N" ancestry of red and yellow as in the Ram, Ric-C and Wol families of Table VII, *b*. The results clearly do not accord with the law of blending inheritance.

It remains to consider if inheritance of hair color follows Galton's law which states that the two parents determine 50 per cent. of the ancestry, the four grandparents together 25 per cent. and earlier ancestry altogether form the remaining 25 per cent.

Taking the 12 families of Tables X, *c*, whose grandparents are all given, we have in the parentage a total of 0 red in 24 parents; and of 5 red in 48 grandparents, or about 10 per cent. Assuming the same proportion of red in the unknown earlier ancestry, we have the total expected proportion of red in the offspring given by the sum

$$\begin{aligned} 0 \div 24 &\times 50 = 0 \\ 5 \div 48 &\times 25 = 2.6 \\ .104 &\times 25 = 2.6 \\ & \quad 5.2 \text{ per cent.} \end{aligned}$$

Actually, there are about 40 per cent. of the red type, and, making every allowance, at least 18 per cent. are to be expected. Five per cent. certainly fits the facts very badly. We conclude, therefore, that Galton's law does not fit the facts as well as Mendel's law and that heredity of hair color is alternative.

E. The Non-transgressibility of the Upper Limit

While the application of the law of alternative inheritance to human hair color lacks something in ideal clearness and precision, one general rule stands out prominently. It is that in the midst of the varying degrees of intensity of the melanic pigmentation the intensity of the melanic pigmentation of the offspring never exceeds that of the more intense parent.

The general intensity relations of melanic hair pigment in parents and offspring are brought out in Table XI.

An inspection of this table shows that, in general, in

TABLE XI.

Grade of Darker Parent.	Hair Color of Offspring.								Red Series.
	Flax.	Yell.	Yell. Br.	Gold.	Lt. Br.	Br.	Dk. Br.	N.	
Flax	4								
Yell.	11	2							
Yell. br.	1	4							
Gold	2			6					
Lt. brown	4	1	2	5	14				3
Brown	11	4	4	4	23	24	5		
Dark brown	4	2	2	5	66	25	58	6	
Black	3	4	5	8	60	37	49	40	4

the melanic series, the grade of intensity of hair pigmentation in the offspring does not exceed that of the darker parent. The only exceptions appear in the "brown" and "dark brown" parentage, where a small percentage of children are represented as of the next darker grade. Many more such cases were in our original records, but wherever the question was asked of the recorder whether the hair of the child, *A*, exceeded in darkness that of the darker parent, *B*, the reply was almost without exception negative. Samples of hair were asked for and these never proved darker in the children than in the parents. A common source of error lies in not disconnecting the effect of a slight grayness in the parent. In one sample of hair from a mother that was reported lighter than the daughter the gray hairs were carefully picked out, when it appeared that the natural color of the hairs of the mother and child were as like as possible. Consequently one is justified in laying no stress on the 11 children out of 600 (less than 2 per cent.) in which the hair color was returned as darker than that of the parents—particularly as despite efforts these returns could not be confirmed. It follows, then, that parents may be assured that their children will eventually have hair as dark as the darker parent or of a lighter tint, but not darker. Consequently, parents with flaxen or yellow hair will have children all alike and like themselves in this respect. But parents with black hair may have children with flaxen hair or with light brown hair

or (because of the masking qualities of black pigment) with red hair.

What is the relation of this principle to the law of alternative inheritance? The latter is only a special case of it. When characters A and B are crossed the more intense character appears in the offspring—the less intense character is recessive—the "heterozygous" children do not exceed the more intense parent. If, now, two such heterozygous persons be mated, one fourth of their offspring show the recessive condition, which by hypothesis is of a lower grade than that possessed by the parents; the remainder of the offspring may attain the grade of their parents; but they will not exceed that grade. This principle of the non-transgressibility of the upper alternative inheritance only, but also for blending inheritance—indeed, it seems to be of universal applicability.

An exception to this rule is exhibited by some heterozygous forms. The cross of a high-combed fowl and a low-combed is a fowl with one intermediate grade of comb. Two heterozygous combs in the parentage throw, *inter alia*, high combs. Not all cases of heterozygous forms constitute exceptions to this law of the non-transgressibility of the upper limit, and human hair color seems, even in the heterozygous condition, to follow the law. The workings of the principle are veiled in some cases of cryptomeric characters, *i. e.*, built up of hidden factors.

Certain important consequences flow from this principle. These one of us has pointed out in a brief communication to *Science*.[3] If the progeny stands on the average in respect to a character at a lower grade than the parents then, if inbreeding is practised, the two parents of the next generation will probably have this character at a lower level than their parents and will produce children having the character less well developed than they have it themselves. If inbreeding be practised for several generations it is clear that in some. at least.

[3] Vol. XXVIII. pp. 454–455, October 2, 1908.

of the children, the character in question would probably become quite degenerate. Since the note in *Science* was published we have read a paper by Feer, to which our attention was called by the title "Der Einfluss der Blutverwandschaft der Eltern auf die Kinder."[4] This paper comes very near to our point of view. After showing that retinitis pigmentosa and congenital deaf-dumbness are the diseases most closely associated with inbreeding the author concludes that they are not so much inheritable diseases in the usual sense as inheritable diseases of degeneration, and depend on degeneration of the embryonic ectoderm. It seems clear from such data as Feer adduces that our general thesis will hold true for many human characters—that inbreeding does not cause them to degenerate, but having a tendency to degenerate, inbreeding will prevent any recovery and, in addition, will hasten the downward tendency from generation to generation. The only way to avoid progressive degeneration is to bring in (usually necessarily from outside) blood with the tendency to produce the characteristic in a well-developed condition.

Combining now the results of the three studies on eye color and hair color and form made by us,[5] it appears that two parents with clear blue eyes and yellow or flaxen straight hair can have children only of the same type, no matter what the grandparental characteristics were; that dark eyed and haired, curly-haired parents may have children like themselves but also of the less developed condition. In the latter case what the proportions of each type will be is, for a fairly large family, predictable by a study of the immediate ancestry.

CARNEGIE INSTITUTION OF WASHINGTON,
DEPARTMENT OF EXPERIMENTAL EVOLUTION,
COLD SPRING HARBOR, N. Y.,
December 1, 1908.

[4] Separate, Berlin, 1907; also "Jahrbuch für Kinderheilkunde," Bd. LXVI.

[5] G. C. and C. B. Davenport, "Heredity of Eye-Color in Man," *Science*, N. S., XXVI, pp. 589–592, November 1, 1907; "Heredity of Hair-Form in Man," AMERICAN NATURALIST, XLII, pp. 341–349, May, 1908.

A MECHANISM FOR ORGANIC CORRELATION[1]

G. H. PARKER

PROFESSOR OF ZOOLOGY, HARVARD UNIVERSITY

THE year 1909 is notable for its many historical associations. It is not only the fiftieth anniversary of the publication of "The Origin of Species," but it is also the centenary of the birth of Charles Darwin and of the publication of Lamarck's "Philosophie Zoologique." To the American its associations with Lincoln are precious memories. But it is not to these historical matters that I wish to refer. Science ever looks forward, not backward, and it is on certain modern aspects of the movements centering about the problem of evolution and especially on those connected with the name of Darwin that I wish to speak.

Although biologists have been familiar with Darwin's theory of natural selection for almost fifty years, it must be confessed that they are only at the threshold of the problem of evolution. That species have arisen by transmutation is now universally admitted, but how transmutation has been accomplished remains at present one of the unsolved riddles. The Lamarckian factors, though possible, must be set down as still unproved. Natural selection, so far as observation and experiment go, seems to play a real part in transmutation, but the extent of its application is still a matter of much uncertainty. Even the recently advanced mutation theory, on which hopes at one time ran high, is coming to assume at best a supplementary rôle. In fact it is evident that the most serious efforts of the past have failed of full accomplishment and it seems likely that the process of transformation is not exclusively dependent upon any single principle, but is of great complexity involving in all probability a consid-

[1] Read before the Boston Society of Natural History, February 12, 1909.

erable number of factors. Of these factors we are only beginning to get glimpses. I believe they will come into clearer view only as we progress in the solution of general biological problems. It is my intention to bring before you very briefly one of these lines of progress and to point out its possible bearing on the problem of evolution.

You are all doubtless familiar with the claim that Darwinism or natural selection is at best only a partial or insufficient factor in evolution. Its actual workings seem to be concerned with the elimination of only the most poorly adapted members of any stock; it is a process that is not closely enough adjusted to call forth those slight but constant differences which every systematist recognizes as the distinguishing marks of a species. To quote from a recent criticism:

> Every student of systematic zoology or botany has a keen realization . . . of the fact that a majority of the distinguishing characters which he recognizes in the various species . . . that come under his eye are of a sort that reveal to him no trace of particular utility.

For this reason it is believed that these characters could not have been produced through natural selection. I hope to show you, however, that we can make the admission implied in this quotation, to the effect that specific characters are not necessarily useful, and still be able to explain their occurrence and fixity through Darwinism.

A general outline of this proposition has already been given by Plate in his consideration of correlation. According to this author the development of a specific character of no special use may take place through correlation, that is, through that unknown law of growth by which an indifferent organ may be so bound up with or related to a useful organ that it, the indifferent organ, is perfected along with the useful organ as this latter is developed or specialized through selection. In this way it is conceivable that a specific character, even though useless, may arise at least indirectly through natural selection. It is to be noted that Plate's conception of the mechanism of correlation is not detailed; in fact, he

describes this principle as an unknown law of growth. It is to this aspect of the subject that I wish to direct your attention.

Only a superficial acquaintance with organisms is needed to make one familiar with many examples of correlation. A hairy integument is always associated with mammary glands; albinism in fur and skin is accompanied with a red color in the eye; and many other examples of correlated characters might be given. The question that we have to consider is the nature of the association in correlated characters and much light can be thrown upon this, I believe, by a study of the ductless glands.

The ductless glands such as the thyroid, the suprarenal bodies and the hypophysis of the brain were originally supposed to be functionless, but recent work has shown them not only to be functional but absolutely essential to the continuance of life. The removal of the suprarenal bodies from a mammal is invariably followed by death within a few hours and the loss of the hypophysis or the thyroid is also fatal though only after a somewhat longer interval. It is thus quite evident that these organs are of vital importance and that the continuance of life is dependent upon their presence. But they are not only necessary for life; they profoundly influence the form and structure of the organism in which they occur. This is best seen in the case of the thyroid. In extreme disease of this gland or after its removal in the higher mammals, the skin thickens and thus produces a misshapen aspect in the features and the extremities, there is a tendency to the loss of hair, and the nervous organs are so affected that the animal sinks into a condition of semi-idiocy (cretinism). Thus there are not only fundamental internal changes, but the external features such as a naturalist might use in describing a species are profoundly modified. Certain external features, then, in the normal animal are correlated with the state of the thyroid and, as disease and experiment show, they fluctu-

ate with the changes in the state of this gland. Our normal skin and features are thus dependent upon the integrity of this internal organ.

The mechanism of correlation between two such organs as the thyroid and the skin has already been somewhat worked out. It is natural to suspect that this correlation is nervous, for both thyroid and skin are supplied with an abundance of nerves coming from a common central organ. But the fact that the symptoms already described as the result of the removal of the thyroid can be checked and even made to disappear by grafting into the animal that has lost its thyroid, a part of a living gland from another animal, shows conclusively that the nervous system is not concerned. The further observation that animals devoid of thyroids may be kept in normal condition by injecting thyroid juice into them or even by feeding them with fresh thyroid glands from other animals, has suggested the idea that this gland produces a substance which makes its way into the blood and is thus carried to those parts of the body where it is needed. It is through this substance that the skin is influenced in that in the absence of this material the skin suffers serious change. The mechanism of correlation between the thyroid gland and the skin, then, consists in a substance produced by the gland and carried in the fluids of the body to various organs, including the skin, whose growth and appearance is thereby modified.

Similar observations have led to a like conclusion concerning the action of the suprarenal bodies and the hypophysis. These organs, like the thyroid, produce substances that make their way into the fluids of the body and influence its structure and action in so profound a way that they are absolutely essential to its continued existence. In the case of the suprarenal bodies the active substance has been isolated and is known as adrenalin. Since these internal secretions have the power of calling forth or exciting very marked changes in the body, they have been given the general name of hormones. It would,

however, probably be a mistake to regard the production of these hormones as limited to a few organs such as the thyroids, suprarenal bodies, etc. The most recent work in this field points to the conclusion that all active organs of the body, nerve centers, muscles, glands, etc., produce hormones which in the blood probably exert extensive influences on the parts with which they come in contact, and examples of this kind are being rapidly discovered. It was formerly supposed that the secretion of the pancreatic juice, which is poured into the small intestine when the partly digested food from the stomach reaches that organ, was dependent upon a nervous signal given to the pancreas from the intestine, but it is now well established, through the brilliant work of Bayliss and Starling, that the action of the acid food on the walls of the intestine produces a hormone, called secretin, which when carried in the blood to the pancreas will cause that organ to secrete. The evidence of this lies in the fact that when a small amount of secretin is injected directly into the blood stream of a mammal, the pancreas, whose nerve supply may have been cut off, will begin to secrete without the presence of food in the intestine. Still more remarkable is the correlation between the mammary glands and the embryo in mammals. It is well known that as the time for the birth of a mammal approaches, the mammary glands of the parent grow in size and structural changes appear preparatory to the secretion of milk. This correlation between the growth of the embryo and the growth of the mammary glands can not depend upon nervous coordination, for the nerves of the embryo have no connection with those of the maternal body. The correlation depends upon a substance, a hormone, produced in the body of the embryo and transmitted to the blood of the mother, whereupon it so influences the mammary glands as to start their growth. The evidence for this lies in the fact that if the extracted juice of a rabbit embryo is injected periodically into the circulation of a virgin female rabbit, her mammary glands can be in-

duced to take on the growth characteristic of the early stages of pregnancy though she is absolutely without young.

Another important set of bodily correlations are those that exist between the reproductive glands and the secondary sexual organs such as the comb, hackles and spurs of the common male fowl. It is well known that if the genital glands of a young male fowl are removed before it has attained maturity, it will fail to perfect its secondary sexual organs and the usual external evidences of maleness may be absent. But if, as Shattock and Seligmann have shown, a small piece of a male gland is grafted into a young castrated male the comb, hackles, and spurs may develop as in a normal bird. It is, therefore, highly probable that the reproductive glands, like the ductless glands, produce hormones by which the development of the secondary sexual organs is determined.

Not only are hormones produced in the adult body, but they are very probably formed during development. Such at least seems to be the condition in the correlated growth of the vertebrate eye and its lens. As is well known, the eyeball in the vertebrate is formed around an outgrowth from the brain; the lens is developed from the skin in such a position as to fit the forming ball. This interesting correlation in position between the external lens and the deep-seated eyeball has been made clear by Lewis who has shown that when the forming eyeball of a given species of frog is covered by grafting over it skin from the abdominal region of even another species of frog, this foreign abdominal skin will begin to form a lens in an appropriate position for the underlying eyeball. Apparently the eyeball gives out a substance, a hormone, that so influences the adjacent skin that, irrespective of its source within certain limits, it forms a lens. Thus embryonic correlations may also depend upon hormones.

These numerous examples show that many organs of the body produce hormones that profoundly affect the

form and structure of many other organs, external as well as internal. And further that these hormones are in some cases absolutely essential to the continuance of life. In short we must consider the interior of every organism as exhibiting an environment to which every organ probably contributes and by which every organ is more or less influenced. The hormones of this environment are the mechanisms of correlation and by means of them one organ influences another. It is no longer necessary to describe organic correlation as an unknown law of growth. It is the dependence of one organ on another through the hormones that the influencing organ produces.

Granting this condition, it follows that natural selection may well be conceived to modify an internal hormone-producing organ, if this organ is of vital significance, and incidentally thus to establish a new internal environment that would so influence the form and external configuration of a given organism that it would be called a new species and yet none of the new external features by which this organism would be described might show the least usefulness.

RECENT ADVANCES IN THE STUDY OF VASCULAR ANATOMY[1]

I. Vascular Anatomy and the Reproductive Structures

PROFESSOR JOHN M. COULTER

University of Chicago

It is perhaps unfortunate that the names applied to the great divisions of botanical investigation shift in their meaning from time to time, but it is inevitable. The content of a subject shifts with the men who put content into it. The morphology of to-day is not the morphology of half a century ago, either in its content or motive; or rather there are several conceptions of morphology existing side by side, some as an inheritance, and others as acquired characters. The older conception of morphology, presented, for example, in the model text-books of Asa Gray, is one thing; and that introduced by the work of Hofmeister, which very slowly made its way into this country, is a very different thing.

This more recent morphology adds to the old knowledge of structures the relation of these structures in a scheme of phylogeny. Its importance lies not so much in the fact that it solves the perennial problem of phylogeny, as in the fact that it calls for the selection and comparison of structures throughout the plant kingdom. It takes the enormous débris of material that has accumulated and sifts it, passing over the trivial, emphasizing the important, and building up the body of knowledge into a structure that has some form. As knowledge advances, the trivial of yesterday may become the important to-day, and *vice versa;* but the building of a structure, upon any plan, is work of a higher order

[1] Papers prepared by request of the Council and read at the Baltimore meeting of the Botanical Society of America.

than the mere collection of building material, and especially stimulates further work to strengthen it or to demolish it.

In the decade we are considering there has come into the morphological camp a powerful ally. For convenience, we speak of it as vascular anatomy; but it is the application of the spirit of the new morphology, the evolutionary morphology, to the vascular system of plants. Before this reinforcement, the modern morphology was dealing almost exclusively with the reproductive structures: sporangia and sex-organs, with their associated structures. It had pressed these structures to the limit of technique, developing morphological cytology. With the vascular system brought into the morphological perspective, the first step was taken towards the inclusion of vegetative as well as reproductive structures. It now remains for some one to begin the organization of the remaining vegetative regions upon the same basis; and then morphology will have its facts fairly before it.

The history of the subject called "anatomy" serves well to illustrate the spirit of modern morphology. It applied to such a mass of facts as are brought together, for example, in DeBary's "Comparative Anatomy of Phanerogams and Ferns," a task which the author regarded as the extreme of drudgery. The older morphology included more or less of this material, for in those days one fact was just about as important as another, and some of these anatomical facts were conspicuous enough for even elementary students to recognize. As is well known, the newer morphology eliminated this whole enormous body of material. The reason is evident and sufficient. It was so completely unorganized that it could not be used in any phylogenetic structure; and the reproductive structures could be so used. All but the blindest morphologists recognized that this vast accumulation of so-called anatomical material would have to be reckoned with some day. It has now developed that the vascular system has been the first thing organized out of the

anatomical rubbish pile, and it has been promptly and warmly welcomed by modern morphology.

The organization of vascular anatomy upon an evolutionary basis came at a most auspicious time, for the phylogenetic lines, guarded only by the anatomy of reproductive structures, had begun to show signs of wavering. Wider researches had begun to dissipate rigid categories into mists. Such veterans of definition as archesporium, sporangium, sporophyll, etc., had been put to flight. Especially did experimental morphology play havoc. It made hereditary structures lose their rigidity, and raised the question whether the hen that sits on the eggs is not more important than the one that lays them. It certainly intensified the conviction that any structure might arise any number of times. This made schemes of phylogeny essentially paper schemes. They were good illustrations of what the phylogenetic succession might have been, but they could carry no assurance of what the phylogenetic succession actually had been.

This whole situation has been steadied, at least morphologically, by the recent development of vascular anatomy, including as it does the enormously important ancient history of the vascular groups, which was largely denied to the reproductive morphologist. The difference between matching forms and investigating structure is nowhere more clearly illustrated than in the recent development of our knowledge of fossil plants. Morphology, therefore, really has another ally that came in company with vascular anatomy, and that is actual history, which must always be reckoned with.

As a result of this triple alliance, what has been the progress of morphology during the last decade? Our subject necessarily limits us to the vascular plants; but it might be said, in passing, that most important progress has been made in bryophytes and thallophytes as well.

Students of gametophytes and sexual organs, of spore-producing members, of the vascular system, of fossil plants, have been investigating with wonderful energy,

and all with phylogenetic relations in view. This has meant comparison at every step; and as a consequence, there is available to-day a wealth of important information such as we have never possessed before. The process of sifting has gone along with the work of accumulation, so that our facts are sorted, and in shape to use. We may not use all this material, but whatever has been collected with a phylogenetic purpose must be reckoned with. One interesting result from this wealth of material has been the loosening up of all our conceptions of structures. No definitions have stood; and our statements to elementary classes are all with important mental reservations. This substitution of a general situation for a rigid definition is also a substitution of knowledge for terminology, and introduces into our phylogenetic schemes a conception of variation that makes them workable.

So many definite lines of attack have resulted in still more numerous schemes of phylogeny. Each investigator naturally regards his own field of work as phylogenetically the important one, otherwise he would not be working in it. A detailed examination, however, of all the schemes based upon extensive investigation reveals the fact that the differences have to do in the main with subordinate features. Certain large conclusions may be regarded as fairly well established, so far as our present information goes. Some of them I may venture to mention, for they represent fairly well the progress of a decade. Of course the progress of largest importance is the fact that so much trained investigation is being directed along so many convergent lines that meet in the problem of phylogeny. Never was morphology so well equipped as it is now. The large results to be mentioned are those concerning which there is substantial agreement; which means results that must have stood the test of morphology, anatomy and history.

Discredit has been thrown upon the cell-by-cell studies of such structures as the embryo, gametophytes, sex or-

gans, and sporangia; and upon the layer-by-layer studies of growing points. This means that an immense amount of detailed work has been swept into the limbo for facts at present useless. Early developmental studies of a few forms seemed to establish definite sequences in cell-divisions and definite functions for so-called generative layers. This kind of research was its own corrective, for as investigations multiplied, definite sequences and functions disappeared in a maze of variation. The definite thing proved to be not the details of development, but the general organization developed. For example, the important facts in reference to the development of the embryo are no longer thought to be the sequence of the first dozen cell-divisions, but the organization of tissue systems and organs. The leptosporangiate sporangium may develop in a great many different ways, but the general result is a sporangium of some definite type. Particularly futile has proved to be the detailed study of the development of independent gametophytes, for they react remarkably to environment, and can be made to do almost anything. At growing points it was once supposed that each cell was predestined to contribute to one of the generative layers, and dermatogen, periblem, and plerome were traced through a mass of indifferent meristematic tissue. After organization, they can be recognized; but there is nothing definite in the details of their origin.

It is generally conceded that no great group of plants has been derived from any other existing group. For example, the origin of pteridophytes from bryophytes is hardly a debatable question. The study of reproductive structures alone made such a connection seem quite reasonable to the scientific imagination. We had even selected the responsible bryophyte forms, and showed how Anthoceros gave rise to the most primitive leafy sporophyte. Now that much other testimony has accumulated, such a connection is too difficult even for a vigorous scientific imagination. Even the staunchest supporter of this connection, and the one who has worked it out in

greatest detail, has acknowledged its improbability. Bryophytes are no longer thought of as having given rise to pteridophytes, but as illustrating here and there the path along which the ancestral pteridophytes may have traveled. Just how we should classify these ancestral pteridophytes makes no difference until we meet them.

The origin of gymnosperms is another conspicuous illustration of the same point of view. Paleobotany has achieved no greater triumph than the discovery of an extinct group of fern-like seed-plants, commonly called pteridosperms, but better called Cycadofilicales. Our knowledge of the group is remarkably complete, so that their connections present no greater difficulties than do those of living groups. Since most of these old seed-plants had been described as paleozoic ferns, it was assumed at first that this was a demonstration that gymnosperms have been derived from ferns. Sober second thought reminded us that ferns as we know them are essentially modern; that the reputed ancient ferns have turned out to be seed-plants; and that the actual ancient ferns, therefore, are unknown. Conceding even that some of the old fern-like plants are ferns, or Primofilices as they have been called, which is very reasonable, the record of the fern-like seed-plants is just as old. The ferns as we know them, therefore, probably did not give rise to gymnosperms, but they may well illustrate stages in the evolution of gymnosperms.

The case is still clearer in connection with the origin of angiosperms. When the Gnetales were first studied, the logic of the morphology of that day suggested that they had given rise to angiosperms, and so the connection with gymnosperms seemed to be established. Nothing could be more clear than that flower, embryo-sac, and even vascular tissue were well on their way to the angiosperm condition. But then Gnetales have no discoverable history, and angiosperms have, not to speak of other difficulties. As a consequence, those who are most insistent

upon establishing a phylogenetic connection between Gnetales and angiosperms claim only that they are lines of parallel development from a common hypothetical ancestry. It is the use of history as a check that has changed our point of view as to phylogeny more than any single factor; and it is the recent vascular anatomy that has given us a trustworthy history.

The transformation in our conception of the inter-relationships of pteridophytes deserves mention. Ever since alternation of generations was recognized, the ordinary fern, with its seductive prothallium, has been generally thought of as the living pteridophyte nearest the bryophyte level. It is now recognized that the Filicales, as a whole, are more clearly connected with seed-plants than is any other group of pteridophytes, and that we must look elsewhere for the most primitive living type of vascular plants. Whether we find them in some of our club-mosses or in Ophioglossum may be an open question for some, which vascular anatomy and history are in a fair way to decide. In any event, vascular anatomy and history have strikingly confirmed, in a general way, the conclusions of the morphology of reproductive parts.

The change of view as to gymnosperms has perhaps been the most striking change of the last decade, and this has been brought about by remarkably aggressive work in several lines of approach, beginning with the discovery of swimming sperms in the cycads and Ginkgo. Of course, the most sensational discoveries since have been the existence of Cycadofilicales and the remarkable strobilus of the Bennettitales. These discoveries have been supplemented by morphological work in almost every genus, anatomical work in all the important groups, and an unprecedented uncovering of the gymnosperm history. Now we recognize the group as starting with fern-like plants, bearing microsporangia and megasporangia as the ferns do sporangia. From this start a strobilus was worked out, whether primitively monosporangiate or amphisporangiate or both is not clear. One line (cycadophyte)

retained more primitive characters in its sexual reproduction and vascular system; another line (Cordaitales), while retaining the more primitive sexual reproduction, developed a more advanced type of vascular system, which has continued in Ginkgoales in one direction, and in Coniferales in the other, associated in the latter with a more advanced type of sexual reproduction.

This gymnosperm situation may illustrate a fact that is becoming more and more apparent. On the basis of the older reproductive morphology the cycads are more ancient than the conifers; on the basis of history the reverse is true. The cycads are relatively modern, but have persistently retained certain ancient features; yet the logic of the older morphology would have insisted that conifers are derived from cycads. It is a fact, therefore, that primitive features are not necessarily a mark of age, even among closely related groups. The testimony of all features must be considered, and this checked up by history, before any rational conclusion can be drawn.

The most baffling tangle of relationships among gymnosperms at present is that presented by the tribes of Coniferales. The perplexity of the situation is due to the fact that as yet morphology, vascular anatomy and history are at variance. Of course, history must determine the actual sequence, and then our contradictory morphology and anatomy can be straightened out. For example, morphologically in Taxineæ are advanced; in wood structure they are also said to be advanced; but they are also reputed to retain the old mesarch structure, which would indicate that they are primitive. When we know what they are historically, we can determine whether this anatomical feature is primitive because the group is primitive, or because this character of the bundle has lagged behind. Of course, these "mesarch" bundles may not be mesarch in the old sense, and the centripetal wood may be explained away; if so, the group will be advanced in all its characters and will not need the testimony of history.

This fact of "lagging behind" is coming more and more into evidence. I do not mean by this that the lagging structures always advance sooner or later, for they may simply persist as veterans. A conspicuous illustration of it is found in the evolution of the microsporangiate and megasporangiate structures of seed-plants. In the most primitive group of seed-plants known, the Cycadofilicales, the microsporangia are still at the fern level, produced in the same relations and of the same general structure as are the sporangia of ferns; while the megasporangiate structure has become a highly organized ovule, which in some way has replaced the sorus. The relations to the sporophyll are the same, but the structure has become very much changed. There is an enormous hiatus in our knowledge in reference to the heterosporous ancestors of these primitive seed-plants, but during all that development of heterospory to the seed-condition, the microsporangia remained practically stationary. Even among the Mesozoic Bennettitales, the microsporangia are still fern-like synangia, although a highly organized strobilus has been developed; and among modern cycads the same persistent lagging of the microsporangia is evident. All this means that no single character, however primitive, can establish the phylogenetic level of a group. All the testimony must be in, and especially the history, before one can feel any reasonable assurance as to conclusions.

The new conception of the monocotyledons is so clearly a triumph of vascular anatomy that the other phase of morphology is hardly entitled to a share in it. And yet, now that it is evident that the monocotyledons are a specialized offshoot from the primitive dicotyledonous stock, many things in the older morphology become clearer. There are those intergrades, as they may be called, between the monocotyledonous and dicotyledonous condition, which have given so much trouble to the pigeon-hole botanist, who insists that a given seed-plant must be a monocotyledon or a dicotyledon. We recognize now

that these intergrades are what might be expected, and they occur in the general region which, according to the vascular anatomist, gave rise to the monocotyledonous offshoot. It has always interested me to see how convinced we become by our own definitions. We have legislated that the last resort for distinguishing monocotyledons and dicotyledons is the cotyledon character; all other characters have been found to be liable to exception. I submit it to you whether any single character selected in this way as final arbiter could not function equally well as a character of last resort. This business of last-resort characters is nothing less than harking back to an artificial system. It is hardly conceivable in these days that such a character can really exist. It is the totality of characters that must place an organism, a most difficult test to apply, but none the less essential. A conspicuous illustration of this situation is that of Selaginella. It is assumed that the last-resort character of a seed-plant is the seed; and yet no definition of a seed can be constructed that will exclude all species of Selaginella and include all seed-plants. Then why is not Selaginella a seed-plant? Simply because its other characters forbid such an association. There is no conceivable reason, therefore, why a dicotyledon may not be monocotyledonous and still remain a dicotyledon, or *vice versa*. The vascular anatomist tells us that one of the surest marks of a monocotyledon is the amphivasal bundle; and at the same time he points out amphivasal bundles among dicotyledons.

I am pressing this point perhaps unduly, but there is a growing tendency that should be checked. This is to transfer groups on a single character, or to propose phylogenetic connections without weighing or waiting for all the characters involved. It is easy to construct a satisfactory scheme based upon one character; it has thus far proved impossible to construct a satisfactory scheme based upon all the characters we happen to know.

The spirit that animates modern morphology is nowhere more evident than in its effect upon teaching.

When this type of work was introduced into the laboratories of this country, almost any available material was used. This material was studied in great detail, important and trivial things being kept at a dead level. The purpose was to train in observation rather than to develop any picture of the plant kingdom. This detailed study meant the handling of a few types. The pedagogical slogan of those days was a few types thoroughly studied. The few types selected were naturally those most available, and by some irony of fate these most available things turned out to be the most unrepresentative types possible. You are familiar with the old list: Spirogyra, standing for green algæ; Marchantia, for liverworts; a leptosporangiate fern, for pteridophytes, and so on. Now all this has been changed. The purpose is to give some conception of the evolution of the plant kingdom, not in detail or in any rigid way, but in general perspective. The threads on which the facts are strung are such as these: the transition from a one-celled to a many-celled body, the evolution of reproductive methods, the origin and differentiation of sex, the acquisition of the land habit, the origin and development of the alternation of generations, the origin of the leafy sporophyte, the evolution of the vascular system, the evolution of the seed, the origin and evolution of the flower. How can "a few types thoroughly studied" illustrate such things or give any such perspective?

This means much illustrative material, carefully selected, and each form used to illustrate some definite and important fact. It is not many types hastily studied, but many types studied carefully for the few points that are really important. The difference between the older view and the recent one, both in teaching and in research, is the difference between an indiscriminate mass of unrelated Details obtained from a few representative forms, and a selected mass of related details obtained from a large number of representative forms.

These somewhat miscellaneous statements may serve

to illustrate the point of view that has been developed, which after all is the significant thing in our progress. It would be tedious and unprofitable to enumerate the long list of important new facts that have been discovered. Besides, these new facts are most of them so technical that any brief reference to them would be intelligible only to those who do not need the information. In closing, I may venture to suggest a future development which seems extremely desirable. The general problems upon which we are now engaged must involve the examination of an enormous amount of material before we can feel any confidence in our conclusions. It ought to be possible to associate investigators or laboratories in a general attack upon any problem conceded to be important enough to justify such a united effort. Whenever this has been done in a laboratory possessing several investigators, the result has been striking. We must begin to combine our detached efforts, the guerilla method of attack, and support individual effort by association. The scheme is only a thought, and the details may make it impossible, but I believe that we have reached a point where something of this kind is demanded for definite and substantial progress.

II. THE PROGRESS OF PLANT ANATOMY DURING THE PAST DECADE

PROFESSOR EDWARD C. JEFFREY

HARVARD UNIVERSITY

THE fascinating problem of the alternation of generations in the higher plants is responsible for the fact that the attention of morphologists, since Hofmeister, has been turned largely to the spore-producing organs and the gametophytes. This tendency can be counted as entirely fortunate, for the closer affinity of the gametophyte with the presumably ancestral forms and the progressive re-

duced and simplified structure, which it presents in the vascular series, has made it particularly suitable for the initial stages of modern morphological development. With the discovery of zoidogamous fertilization in Cycas, Ginkgo and the lower fossil gymnosperms, the revelation of the remarkable mode of fertilization in the Araucarineæ, simulated at least in the Podocarpineæ, the uncovering of the phenomenon of breech fertilization in the lower Amentiferæ and the elucidation of other striking phenomena connected with the male gametophyte, we have come to realize that it is the male sexual generation and the sporogenous apparatus, producing it, which carry the highest phylogenetic interest. The origin of the seed from the megasporangium, although beyond question on general morphological grounds, still largely lacks illuminating facts to lighten the darkness of its past.

The more complicated sporophytic generation of the higher plants, except as to its special sporogenous structures, has much more recently been attacked by evolutionary morphologists. Its very complexity, however, and the possibility of following its structures into the remotest past, make it of the greater importance from the standpoint of the theory of descent. The evidence derived from its study serves, moreover, to control, amplify and enrich the conclusions reached from the standpoint of the morphology of the gametophyte alone. We have, accordingly, begun to realize that the anatomical examination of the sporogenic organs of vascular plants is quite as important as the cytological study of the process of sporogeny itself, and that the fern-like mode of fertilization obtaining in the lower gymnosperms, living and extinct, has its not less important or significant equivalent in the presence of cryptogamic or centripetal primary wood. In fact, with the realization of the importance of the sporophytic generation in the higher plants, we are now for the first time in a position to begin our phylogenetic bookkeeping by double entry, with greatly added security as to the final accuracy of the balance we may strike.

Perhaps nowhere is the advantage of morphological bookkeeping by double entry more clearly illustrated than in the case of the conifers. Forming with the other living gymnospermous species a restricted but illustrious "four hundred," they have quite held their own in botanical interest, in spite of the overwhelming numbers and importance of the modern mob of angiosperms. The older and entirely superficial morphology, led to the conclusion that simple forms and structures are more primitive. On this basis the conclusion was reached that those simple and coneless conifers, the Taxineæ or yews, are the oldest and that the pines or Abietineæ, with their very complicated cone-structures, are most modern. It has, moreover, been inferred that the coniferous tribes represent a series of progression beginning with the yews and ending with the pines. The microscopic study of the gametophytes began the disintegration of this system. The discovery of zoidogamous fertilization in Ginkgo, which in Engler and Prantl's Natürliche Pflanzenfamilien, you will find included with the yews, made it at once apparent that this remarkable genus, sole survivor of an abundant stock, once flourishing through the entire northern hemisphere, could not be included under the Taxineæ, or link the latter with the still more ancient Cordaitales, confined to the Paleozoic. Thus deprived of the reputation of an illustrious ancestry, the yews have since been disrespectfully kicked up the phylogenetic stairs by the younger generation of gametic morphologists. A corresponding but reversed process has in the meantime taken place at the other end of the coniferous series. It has been shown by the gametophytic morphologists, that the sexual generations of the pine tribe are more complicated, and for that reason more primitive in the reduced members of the alternation, than any other conifers, characteristically found in the northern hemisphere. From the sporophytic side it has been shown that the cone-structure of Pinus affords an anatomical explanation of the strobilar organization of the other tribes of conifers on the basis

of commonly accepted principles of reduction and adhesion. Further, it has recently been discovered that the leaves of the ancestral pines (Prepinus) had the same cryptogamic type of centripetal wood-bundles, which are found in the Cordaitales, universally regarded as the Paleozoic stock to which the conifers as a whole are most nearly allied. There is further evidence of the antiquity of the Abietineous or pine tribe based on important experimental data and on the origin of coniferous pitting, which need not be entered upon here. If, in accordance with the facts very briefly indicated above, we cast up our phylogenetic balance by double entry for Pinus, we find it on both sides overwhelmingly in favor of the superior antiquity of the Abietineæ, or pines, as compared with the Taxineæ, or yews. It would take much too long to cast even hastily the balances for the remaining tribes of conifers and in the case of those at present mainly or wholly confined to the southern hemisphere the data are as yet not complete. Even though the books are not yet ready to be opened for the final judgment, the results of recent morphology on both the gametic and sporophytic sides make it clear that the conifers, contrary to the conclusions of the old superficial morphology, are a series of reduction and not one of progression and that their most complicated forms are consequently the oldest and those of simplest guise the most modern.

One of the most striking confirmations of the truth of the theory of organic evolution is found in the recapitulationary phenomena of animals. The colt, for example, in the course of its individual development passes through the phases of progressive loss of digits, presented geologically by the equine stock from the Mesozoic to the present. The young mammal in its earlier stages of ontogeny possesses the gill arches and the segmented musculature of the fish. In the principle of recapitulation presented so clearly in the development of animals, our zoological brethren may fairly claim that on their side of the house the truth of evolution is declared by the

mouths of babes and sucklings. Although our seedlings, unlike the sucklings, are dumb, they are by no means speechless. One of the most striking triumphs of modern plant anatomy is to have discovered many examples of recapitulationary confirmation of the principle of evolution. To take a modern and striking instance, let us consider our common and flourishing northern genus, the oak. You are all familiar with the very broad rays which constitute so ornamental a feature of the structure of oak wood. You are likewise doubtless aware that the weight of paleobotanical evidence speaks for the derivation of the oaks from ancestors resembling the chestnuts since the older oaks approach the chestnuts both in their foliage and in their reproductive organs. The wood of the chestnut differs, however, strikingly from that of oaks by the entire absence of large rays. It has been recently discovered that certain oaks of the gold-gravels (Miocene Tertiary) of California have their large rays composed of aggregations of smaller rays. In the seedlings of certain of our existing American oaks this condition, interestingly enough, is a passing phase, which by the loss of the separating fibers in the congeries of small rays produces the characteristic large rays of the adult. This condition of development in the living oaks is all the more significant because in certain breech-fertilized or chalazogamic amentiferous trees of the present epoch, such as the alder, the hazel and the hornbeam, such aggregated so called false rays are a permanent feature of structure in the adult. From the anatomical side, in the case of the lower Amentiferæ, we have accordingly at the same time an interesting example of the general biological law of recapitulation and a confirmation of the view expressed by Treub and Nawaschin, on evidence from the gametophytic and reproductive side, that the breech-fertilized Amentiferæ are relatively primitive angiosperms.

Perhaps the most valuable service which anatomy is rendering to phylogeny and evolution is in connection

with the elucidation of the affinities of extinct plants. Certain cryptogamic trees of the Paleozoic, the Lepidodendrids, Sigillarians and Calamites, were, for example, long regarded by competent botanists as seed plants on account of their arboreal habit. The anatomists stoutly maintained, however, that from the structure of their primary wood they must be cryptogams. The subsequent discovery of their reproductive structures entirely confirmed the anatomical view. More recently from the study of the anatomy of certain fern-like plants with secondary growth, from the Paleozoic, English and German anatomists reached the conclusion that they were gymnosperms and allied at once to the ferns and to the cycads. Within the past decade, the brilliant discoveries of Oliver, Scott, Kidston, Grand'Eury and David White in regard to the nature of the reproductive organs of these plants, prophetically dubbed by Potonie, the Cycadofilices, have confirmed the truth of the anatomical view as to their affinities in every particular. Let us take a still more modern instance. There are present in the later Mesozoic strata huge quantities of impressions of the cones and leafy twigs of conifers. These have been referred on features of superficial resemblance to a number of genera of living conifers as well as to others not represented in the existing flora. Since they are very numerous, let us take one typical example, which is at the same time significant. Many species of Sequoia have been described from the upper Jurassic and the Cretaceous beds, on the evidence of the impress upon the stony or argillaceous matrix of their cones and leafy branches. Dr. Arthur Hollick and the present speaker have been fortunate enough to secure by new methods of isolation, material of these cones and twigs, with internal structure preserved. The anatomical features of both reproductive and vegetative organs of the remains in question, show beyond any possible doubt that they belong to a tribe of conifers at present confined to the southern hemisphere, the Norfolk Island and Kauri Pines

or Araucarineæ, and have not even the slightest affinity with the living genus, which externally they so strikingly simulate. The reference of the fossil genus just described to its true affinities as well as similar results in the case of a large number of other Mesozoic conifers, likewise erroneously placed in the system, leads to important general conclusions in regard to the evolutionary history of coniferous gymnosperms, which are too lengthy and too technical even to be mentioned here.

But it is not only in connection with extinct plants that anatomy has shown itself the useful servant of phylogeny. The enforced use of anatomical criteria in the case of fossil forms, where such evidence is absolutely indispensable, has resulted in a new and broader point of view in general botanical morphology. Within the decade we have begun to realize fully the great constancy of fibrovascular structures. This may perhaps be best exemplified by a special case. Superficially there is no organ of the plant more prone to vary extremely, within near lines of affinity, than the leaf. If, however, we look within, it presents anatomical features of great constancy. In the case of the leaf, perhaps the most hopelessly variable feature is its size. Anatomically, however, there are just two sizes of leaves, large leaves (megaphylls) and small leaves (microphylls), which are absolutely characterized by their anatomical relations. The foliar strands of the megaphyll, or large leaf, pass off from the woody cylinder of the stem, leaving corresponding gaps in its wall. Those of the microphyll, or small leaf, equally constantly leave no such gaps in their exit from the woody cylinder. It is even possible to divide the whole vascular series into two clean-cut phyla on the basis of the anatomical features of leaf size, viz., the Pteropsida with, anatomically speaking, large leaves, including the ferns, gymnosperms and angiosperms and the Lycopsida, structurally speaking, small leaved forms including among living plants only the club-mosses and horsetails.

I have tried to show above, with all necessary brevity, that the services of anatomy to phylogeny and the doctrine of descent during the past decade have been neither few nor unimportant. Perhaps the most important general result of recent work in the modern morphological field, not restricting it, of course, to anatomy, may best be expressed in the words of the eloquent and philosophical apostle to the gentiles, viz., that the things seen are temporal, while the things unseen are eternal. You may think that I have too much emphasized the importance of internal morphology. One example will serve to show that I have not. You are all familiar with that great German work on the morphology (or, as its author prefers to call it, the organography) of the higher plants, which not very long ago appeared in a *traduction de luxe* from the Oxford University Press. If you scan it from cover to cover, I do not believe you will find a single figure of the fibro-vascular structures. Not even the proverbial halfpenny's worth of bread is present to qualify the oceans of sack. It is not surprising that we should hear from such a source a strong note of morphological pessimism. On a recent occasion in our own country, the distinguished author of the work in question compared the task of his science to that of Sysiphus, of classic fable, condemned to roll up the mountainside a stone which continually rebounds. We may confidently expect that the morphology of the future, distrusting the superficial anfracutosities of the steep, will bring the profitless rolling stone to rest in the very heart of the mountain itself.

SHORTER ARTICLES AND CORRESPONDENCE

A NOTE ON THE DEGREE OF ACCURACY OF BIOMETRIC CONSTANTS

The statement is frequently made, either in comment or criticism upon biometric work, that such work is often caused to take on an unwarranted appearance of precision and exactness by the keeping of a larger number of decimal places in the tabled constants than the character of the original data justifies. The contention is made that under no circumstances whatsoever can any statistical constant be more accurate than the data on which it is based. It is held that if one makes a series of measurements accurate to a tenth of a millimeter, it is a logical absurdity to table the mean or standard deviation deduced from these measurements to hundredths of a millimeter. Not only is this contention made from time to time by biologists, but occasionally even by a mathematician, a fact which of course tends strongly to confirm the biologist in his opinion. Thus Engberg[1] specifically says (p. 11) referring to mortality statistics: "The constants can not be more accurate than the data on which they are based."[2]

The reply which the statistician makes to the criticism that constants can not be more accurate than the data on which they are based is generally that the accuracy of a statistical constant depends not alone on the accuracy of the original measurements but also upon the number of such measurements. Further it is pointed out that, because of this fact, it is possible to deduce from measurements known to be individually inaccurate constants of a high degree of accuracy, *provided* that the errors in the measurements are unbiased (that is as often in excess as in defect of the true value) and that there are enough of the data. Finally the statistician contends that the only proper measure of the accuracy of a statistical constant

[1] Engberg, C. C. The Degree of Accuracy of Statistical Data. *Univ. of Nebraska Studies*, Vol. III, No. 2, pp. 1–14, 1903.

[2] In passing it may be said that any one who is sufficiently interested in the phenomenon of a professional mathematician taking this curious position will find an entirely adequate and satisfactory discussion of the matter in *Nature*. Vol. 69, p. 93, where Engberg's paper is reviewed.

(always assuming that the original data are not collected in a deliberately dishonest or biased manner) is its "probable error." Unfortunately this statement of the case appears not to carry conviction to the non-statistical worker. It has seemed to the writer that if the assertion made by the statistician regarding the point under discussion is true, it ought to be possible to demonstrate it in such a manner as to carry conviction to anybody.

With this object in view the experiment to be described was tried. Some time ago the writer measured for another purpose the lengths of 450 hens' eggs. The measurements were made with a large steel micrometer caliper manufactured by Browne-Sharpe & Co., reading directly to hundredths of a millimeter. The utmost care was exercised in the making of the measurements; they were all made under the same conditions as to light, temperature, etc.; the caliper was held in a specially constructed stand to get rid of the error arising from expansion and contraction if it is held in the hand; the micrometer screwhead was fitted with a ratchet which mechanically insures that the same pressure shall be exerted on the object in every case; all measurements were made by the same observer who has had considerable experience in close micrometer measuring. The maximum length was the thing measured. There is every reason to believe that these measurements to hundredths of a millimeter are as accurate as it is possible to make them with the instrument used. This being the case all will agree that any statistical constant deduced from them can be held to be accurate to hundredths of a millimeter at least. Now let it be supposed that these eggs had been measured only to the nearest millimeter instead of to the nearest hundredth of a millimeter. By how much would the statistical constants deduced from the "millimeter" data differ from those deduced from the "hundredth millimeter data?"[3]

To answer this question it is necessary to calculate some statistical constant for the two sets of data. The mean was chosen as the simplest possible constant. The actual measurements to hundredths of a millimeter were used as one set of data. The "millimeter" data were obtained by discarding the decimals of the original measurements. In this discarding a record was raised 1 mm. whenever the decimal portion of the original

[3] The biometrician will, of course, recognize that the problem here involved is the same as that of the influence of the fineness of grouping on the value of constants.

figure was .51 or greater. When the decimal part of the record was .49 or less the integral part stood unchanged. In the 450 measurements there were six cases in which the decimal portion of the record was exactly .50. In one half of these cases the record was raised 1 mm. and in the other half was left unchanged, when the decimals were discarded. This is obviously the only fair way of dealing with such cases since, for example, 51.50 is exactly as near to 51 as it is to 52.

The original measurements and the "millimeter" data after discarding the decimals were then each added and re-added with a calculating machine. The resulting sums were:

When the measurements were kept to the nearest hundredth of a mm.	When the measurements were kept to the nearest whole mm.
25,341.95	25,346

Dividing each of these figures by the total number of cases, 450, we get for the means the following:

Mean from "hundredth mm. data"	Mean from "millimeter data"
56.315	56.324

The difference between these two figures is .009. That is, there is no difference between the two averages until the third decimal place is reached. To two places of figures both means are 56.32. But this can only mean that the mean or average obtained when the records are made only to the nearest millimeter is *more* accurate, by two places of decimals, than the data on which it is based.

In interpreting this statement of fact it must not be held to signify that biometric measurements should not be made with the greatest attainable degree of accuracy. Because statistical constants, when the number of cases dealt with is large, are more accurate than the data on which they are based gives no excuse for rough measuring. The reason for this, of course, lies in the principle, which actual experience shows to be correct, that the finer and more accurate the measuring the less chance of the data being unconsciously biased. Statistical constants can only be more accurate than the original data when the data are strictly unbiased. The "applied psychology" of practical measuring teaches that unconscious bias goes out of the records just in proportion as the measurements are made finer.

RAYMOND PEARL.

MAINE EXPERIMENT STATION.

PURE STRAINS AS ARTIFACTS OF BREEDING

Students of the minute anatomy of plant or animal tissues are on their guard against artifacts. Chemical reagents often contract or coagulate the protoplasm or cause the precipitation of granules or crystals. The artificial results of the methods of preparation have to be distinguished from the normal structures of the protoplasm. Precautions are equally necessary in the study of evolution and heredity, to avoid mistaking artificial products of breeding for typical conditions.

Close-bred, uniform groups of plants and animals form the basis of the idea of "pure strains," "elementary species" or "biotypes." If the descendants of the same parents appear sufficiently alike the strains are said to be "pure." General inferences regarding heredity and evolution are being based on the assumption that this uniform "purity" represents a natural condition. Yet there can be no doubt that the methods used in maintaining and testing the purity of strains are calculated to produce an artificial uniformity of characters, commonly accepted as the proof of purity.

If the habits of a plant will permit, the readiest method of securing uniform progeny is by vegetative propagation. Nevertheless, the idea of pure strains is not usually connected with vegetative varieties, for it is recognized that uniformity lasts only while vegetative propagation is continued. As soon as seeds and seedlings are grown the natural individual diversity reappears. The vegetative propagation only conceals the inherent diversity by devices that avoid the production of seedlings.

The uniformity of groups of seedling plants is of the same artificial nature as the uniformity of vegetative varieties. Particular methods of reproduction are necessary to secure uniform seedlings—methods which may not be essentially different from those represented by cuttings or offshoots. Plants grown from buds or cuttings have only one parent, and the same is true of seedlings produced by self-fertilization. It is only when conjugation is restricted to cells of the same individual or of closely related individuals that uniform seedlings are obtained. The external formalities of conjugation are preserved, but without the essential diversity of descent which gives conjugation a physiological significance.

The uniformity of varieties of wheat and other strictly self-fertilized plants depends as closely upon self-fertilization as

the uniformity of vegetative strains upon vegetative propagation. As soon as individual wheat plants are crossed, even inside the same variety, a wide range of diversity reappears. Self-fertilization, like vegetative propagation, brings uniformity by suppressing the inherent tendencies to diversity. Pure strains continue to seem pure as long as only one set of characters is brought into expression, but the latent diversities do not cease to be transmitted, and at once reappear when hybrids are made, or selection is relaxed, or the plants are transferred to new conditions.

It is true that uniformity like that of the pure strains of domesticated varieties is sometimes found in nature, but even this does not prove that uniformity represents a truly normal condition of reproduction. Having learned that artificially restricted descent produces uniformity in domesticated varieties, it is easy to understand that natural conditions of close breeding can also produce uniformity.

The methods of reproduction that yield uniform offspring often appear very effective from the environmental standpoint, but this only shows the more plainly their physiological inferiority. All indications point to the probability that long-continued vegetative propagation, self-fertilization or close breeding bring the same deterioration, sterility and ultimate extinction to wild types as to domesticated varieties. It does not appear that the vigor and fertility of organisms can be permanently maintained by the methods of reproduction required for pure strains. Free interbreeding among diverse individuals to form a continuous network of descent is the natural relation of the members of species.

The physiological inferiority of pure strains forbids our acceptance of theories of evolution and heredity based upon the idea of uniformity. Neither uniformity itself nor the attendant phenomena of mutation and Mendelism represent primary biological facts, typical of organic existence and evolutionary progress. The restriction of descent to closely similar and closely related individuals is a change from a natural state to a relatively artificial, atypical condition. Darwin saw in the facts of Mendelian inheritance a definite evidence of the abnormality of mutations, but the significance of this relation is not fully appreciated until we perceive that the uniformity of pure strains already marks a first step toward degeneration.

WASHINGTON, D. C.,
February 10, 1909.

O. F. COOK.

NOTES AND LITERATURE

HEREDITY

The Nature of "Unit" Characters.—One of the clearest presentations of Mendelian principles that has appeared recently is that of Dr. E. Baur in *Beihefte zur Medizinischen Klinik*, Vol. 4, 1908, pp. 266 et seq. He has given special attention to inheritance in crosses between the various varieties of *Antirrhinum majus*. He states that he knows 250 distinguishable varieties of this species, but he has never found amongst them characters that do not obey Mendel's law. He has demonstrated fifteen pairs of characters for the species, which is more than the number of chromosomes present, from which fact he concludes that the chromosome as a whole can not be considered as the basis of Mendelian unit characters. Others have cited as a basis for the same belief that more character pairs are known in Pisum than there are chromosomes present in the cells. This conclusion is not a necessary one, as is seen in the following. Speaking in a general way, the chromosomes are present in pairs of homologues. For each pair in the cells of a given individual there is a homologous pair in the cells of other individuals of the species. For convenience we may designate one of these pairs as A chromosomes, a second as B chromosomes, etc., the same pairs as a rule being found in different individuals of the same species.

If we consider the species as a whole, the number of pairs of A chromosomes is equal to the whole number of cells in all the individuals of the species. It is conceivable that, since certain of these A chromosomes may trace back thousands of generations before their ancestral lines unite, it is possible that there may be an indefinite number of subgroups of A chromosomes in the species, and that each subgroup may represent a heritable difference from other groups. But each of these subgroups would represent a Mendelian character. Hence, there might possibly be an indefinite number of Mendelian character pairs in a species having only a single pair of chromosomes.

But these characters could not all exist in one individual. Only two of the subgroups could be present together. Hence, in such a species, only two independent (not correlated) domi-

nant characters could be present, and these two would present a case of what Bateson calls spurious allelomorphism, for they would separate from each other in the reduction division.

It is clear, therefore, that the presence *in a species* of more Mendelian character pairs (presence and absence constituting a pair) than there are chromosomes does not prove that Mendelian characters do not appertain to the chromosome as a whole. If, however, in a species having one pair of chromosomes we could get *into a single individual* more independent character pairs than two, or if we can get even two dominant characters that are independent of each other, and not allelomorphic to each other, then we should have proven that Mendelian characters do not appertain to whole chromosomes. In general, if, in a species having 2n chromosomes, we can bring together in a single individual more than n independent dominant characters, no two of which are allelomorphic to each other, then it would be proved that Mendelian phenomena are not simply phenomena of the chromosomes. In a recent communication to the writer, Dr. Baur recognizes the justice of the above point of view and hopes to be able to test the matter in the near future. Dr. Shull will make a similar test at the Cold Spring Harbor Station. This, it would seem, is a simple and direct method of testing the validity of the theory advanced by many investigators, that the chromosome itself is the basis of the so-called unit character.

Even if this theory should be substantiated, it does not follow that the chromosome represents a unit character in the sense in which the term unit character is understood by most Mendelists. Shull has very justly pointed out[1] that "there is no evidence of the existence of a pair of internal units (allelomorphs)." The term "unit" has been applied to Mendelian characters on the assumption, which I regard as untenable, that there is in the germ plasm a definite organ set aside for each hereditary character. An elaborate theory of inheritance and evolution (De Vries) has been erected on this assumption. Mendelian phenomena can be explained in a wholly different manner, and one which is more consistent with the idea of the chemical basis of life processes, as the following illustration shows.

Let us designate the chromosome pairs in our common domesticated cattle as A, B, C, . . . L. Let us assume that the chromosomes in each of these pairs are capable of several types of metabolic activity, and that each of them, by its action on the nutritive materials furnished it, gives rise in the cell to as many

[1] See *Science*, February 12, 1909.

metabolic products as it has metabolic activities. Doubtless some of these products will be similar for a number of chromosomes. We may thus represent the chromosomes and their functions:

(AA) — functions a, b, c, d,
(BB) — " b, c, d, e.
(CC) — " a, b, d.
(EE) — " a, b, f.
Etc. Etc.

Now, of the numerous B chromosomes in the species, some may perform the function e in a manner differing from the others. This function may fail entirely in some of them. Let us assume that the production of horny substance requires that the functions a, b, e and f shall be normal. If in a given group of individuals the function e fails, which function may represent the production of a given chemical substance in the cell, then horns fail to develop. Individuals without horns would thus be represented as follows:

(AA) — a, b, c, d.
(BB) — b, c, d.
(CC) — a, b, d.
(EE) — a, b, f.
Etc. Etc.

Omitting from consideration those chromosomes which are not concerned in the hereditary difference in question and remembering that the poll character is dominant, the heterozygote between the horned and polled forms would be

B — b, c, d, e; B — b, c, d (heterozygote polled).

Generation F_2 would consist of

1. B — b, c, d, e; B — b, c, d, e (horned).
2. B — b, c, d, e; B — b, c, d (heterozygote polled).
3. B — b, c, d; B — b, c, d (homozygote polled).

or three polled to one horned. Thus we derive the well-known Mendelian ratio entirely independently of any idea of unit character in the germ plasm. Rather we assume that horns are due to the presence in the cell of certain substances each produced by the chromosomes, as a result of their *chemical constitution;* and the poll character is due to the failure of a *single* chromosome to perform a particular function. When a hereditary difference between two varieties is thus due to a difference in a *single* set of homologous chromosomes, such difference will be-

have as a simple Mendelian character. If it be due to differences in two sets, it will behave as a compound character of two factors, and so on.

All known Mendelian phenomena may thus be explained as due to differences in the chemical constitution of the chromosomes in different groups. It is thus seen that Mendelian phenomena lend no support to the theory that each hereditary character is represented in the germ plasm by a separate entity.

The question as to the nature of the chromosome differences which are thus seen to be able to account for the phenomena first interpreted by Mendel will be considered at another time. The differences between the metabolic activities of homologous chromosomes here assumed may be due to differences in the relative amounts of given substances in the chromosomes concerned, or they may be due to differences existing in different *regions* of the chromosomes. In the present state of our knowledge of the chromosomes we are not ready for any theory on this point. Should Shull or Baur succeed in getting into a single individual more independent (neither correlated nor allelomorphic) dominant characters than there are chromosome pairs, then we shall at least know that the chromosome as an individual structure is not responsible for Mendelian characters. This is the one question which must be settled before Mendelian theory can make further progress.

Much recent work has been done which bears on the relation between chromosomes and hereditary characters.

First of these should be mentioned the important contribution made by Professor E. B. Wilson, published in *Science*, January 8, 1909. This paper is so accessible that it is unnecessary here to review it in full. Suffice it to say that Professor Wilson and his students have demonstrated an important relation between sex and certain chromosomes and chromosome groups. In general, the cells of the species studied contain an "X-element" which in some species consists of one chromosome, in others of two, in others three, and in one species of four chromosomes, but which acts as a unit in the reduction division; *i. e.*, all the chromosomes of the "element" pass to the same pole. In all the species studied, the cells of the female contain two of these X-elements, while those of the male contain but one. The males of some of the species contain no homolog (synaptic mate) for this element, but others contain an element which Wilson calls the Y-element, with which the X-element pairs in the reduction division. In every case the Y-element, when present, consists of a

single chromosome. In every case, therefore, the female is homozygote for the X-element, while the male is heterozygote either for X and Y, or for X and absence of X. Wilson shows that the above relations hold in a wide range of organisms, and suggests that it may be a very general relation. There are reasons however, for suspecting that the relation is not the same for all organisms. In a previous paper[2] I pointed out a number of cases which indicate that the female may be heterozygote and the male homozygote for sex, though some of the phenomena cited may be explained on a different basis. Miss Durham and Miss Marryatt[3] have recently worked out one of the cases referred to in my former article, which is a case in point. In certain strains of canaries, black-eyed females mated with red-eyed males give only black-eyed males and red-eyed females. This may be explained, as the authors point out, by assuming a correlation between eye color and sex. Letting X represent the chromosome element characteristic of the female and Y that of the male, assuming that Y is responsible for black pigment in the eye and that in some individuals Y has lost the pigment-producing power, the facts are rendered intelligible by the following assumptions regarding the gametic constitution of the types:

Black-eyed female = X Y–B, in which Y and B belong to the same chromosome element.

Red-eyed male = Y–b Y–b, where the function B is absent.

Here the females produce two kinds of eggs, namely, X and Y–B, while the males produce one kind of sperm (Y–b). This gives progeny of two types, namely, X Y–b (red-eyed females) and Y–B Y–b, black-eyed males. All the phenomena cited by Miss Durham and Miss Marryatt are explicable by assumptions similar to the above, though the occasional occurrence of black-eyed hens in the mating of black-eyed hens with pink-eyed cocks renders it necessary to assume that in some hens the X-element can also give rise to black pigment, or at least stimulate its production in some other element.[4] The facts cited in my previous paper regarding the inheritance of the bar character in the plumage of poultry further indicate that the female and not the male may be heterozygote for sex, as do also Doncaster's results

[2] AMERICAN NATURALIST, September, 1908.

[3] Rep. IV, Evol. Com., Roy. Soc.

[4] The gametic constitution here assumed is not that of the authors. They assume that *B* and *Y* are separate, but that *B* is "repelled" by *X*, thus giving the same results as above.

with the moth Abraxas. It is hoped Professor Wilson may be able to make cytological studies on some of these cases.

The fact that such characters as eye color in canaries, barring in poultry, and melanic types in Abraxas may be coupled with sex points strongly to the chromosomic nature of these characters. The work of Professor R. R. Gates, and that of Miss Annie E. Lutz on the chromosomes of Œnothera points strongly to the assumption that chromosomes are the elements with which we have to deal in the study of hereditary characters. Their results indicate that mutations of the De Vriesian type are due to accidents in mitosis. Miss Lutz remarks:[5]

> The numbers of chromosomes are closely associated with external characters in the first and last, and probably also in the second group.

Professor Gates has also expressed the opinion that abnormal chromosome behavior may account for the mutation phenomena observed by De Vries. It seems probable, therefore, that mutations of this character do not represent what we may call normal evolutionary changes, but that the latter must be sought in changes in the chemical constitution of the chromosomes.

W. J. SPILLMAN.

ENVIRONMENT

The Effect of Environment upon Animals.—"Katy-did, Katy-didn't" seems to continue to be a fair summary of the situation with respect to the heredity of acquired characters and the part played by environment in evolution. Wallace wrote in the *Fortnightly Review* (January, 1908) restating his belief in natural selection and recommending a careful study of Reid's "The Principles of Heredity" and Ball's "Are the Effects of Use and Disuse Inherited?" Rev. Henslow followed his advice and has published a short, suggestive and very readable book[1] on "The Heredity of Acquired Characters in Plants," in which he states with even more assurance than before the conclusion of his "Origin of Plant Structures," that "the Origin of Species is due to the joint action alone of the two great factors of evolution—*Variability* and *Environment*—without the aid of natural selection." This additional assurance seems to be the result of the growth of the ecological school of botanists and his belief that ecologists are "all at one" in accepting the fact that evolution in plants is the result of the effects of the environment which *can* become heredity.

[5] *Science*, February 12, 1909.

[1] London, John Murray, 1908, 107 pp.

In 1876 Darwin had become a true ecologist. In this year he wrote to Professor Moritz Wagner as follows: "The greatest mistake I made was, I now think, I did not attach sufficient weight to the direct influence of food, climate, etc., quite independently of natural selection. When I wrote my book and for some years later, I could not find a good proof of the direct action [*i. e.*, in producing definite variations] of the environment on the species. Such proofs are now plentiful [Henslow says 'universal']."

Plant ecologists . . . are accepting "Adaptation" by response as a *proved fact*. . . . A complete change of front has taken place within the last twenty years, but as Darwin himself was the first [?] to propound this view, I called it "The True Darwinism."

Zoologists have been rather behind the botanists in ecological work, but the zoological school of ecology is growing and it does seem true that the more organisms are studied with regard to their relations to their environment, "at home," the stronger becomes the belief in the importance of environment in evolution. Whether this is "True Darwinism" or something else is immaterial, only so it be true.

The most serious difficulty has been to get a good way of accounting for the inheritance of characters produced by the environment. Cunningham[2] seems now convinced that this difficulty is removed by "hormones," or internal secretions, retracting his former idea that the nexus between secondary sexual characters and the gonads is nervous. Starling's proof that the growth of mammary glands in an unimpregnated rabbit is caused by injection of extracts of fœtuses from pregnant rabbits is given as an illustration of the working of hormones. Applied to the development in phylogeny of horns, for example, it is supposed to work about as follows:

Since the development of the somatic sex-characters is due to the stimulation of the cells by a hormone derived from the gonad, it is conceivable that the gametes may be affected by the internal secretion of the somatic cells whose development constitutes the sex-character. It is quite possible that the hormone in the case of the gonad, perhaps in all cases, is merely the waste product of metabolism occurring in the cell-multiplication. Whether this is so or not, the somatic sexual structure, such as the antler, would naturally excrete into the blood special substances, and these being in the blood the gametes would be multiplied and developed under their influence. We can not suppose that all cells or parts of the body produce living gemmules which are collected in the germ-cells, but we have reason to conclude that all

[2] "The Heredity of Secondary Sexual Characters in Relation to Hormones, a Theory of the Heredity of Somatogenic Characters." *Archiv Entwicklungsmechanik*, XXVI, 3, 1908.

parts of the soma give out to the blood specific chemical substances which have a marked effect on development, and in presence of which the gametes develop. If we suppose that certain parts, *e. g.*, the frontal periosteum in the ancestors of deer, are stimulated to hypertrophy by external stimulation, this entails an increase in the hormone produced by this part of the body, and this hormone will affect the protoplasm of the gametes which obtain their nourishment from the blood. Mendelians and the majority of modern authorities on heredity and evolution assume that certain material parts of the gametes correspond and determine particular parts and characters of the soma, and therefore the hormones derived from these parts of the soma may well have an influence on the corresponding determinants in the gametes. . . . I must of course assume different hormones for different bones of the body, so that increased hormone from the frontal bone causes modification of the determinant corresponding to that bone, not of bone in general. Thus we have a material chain of influence from a particular part of the soma to the gamete, and from the latter to the corresponding part in the next generation. Whether this suggestion be true or not, it at least destroys the contention that we can not form a conception of the means by which a change in the soma can effect a corresponding part in the descendant. The hypothesis I have suggested would explain ordinary adaptations more easily than secondary sexual characters. It might be applied, for instance, to the hoofs, toes and legs of Ungulata. I hope soon to test my hypothesis by physiological experiment. If there is an influence from the parts of the soma to the determinants of gametes, then an ovary of one kind of animal grafted into another, ought to show an alteration in the character of the individuals developed from that ovary.

The author has apparently not seen an account of Guthrie's work of grafting ovaries. However, it is far from certain, or believable, that specific hormones are given off when the head is rubbed, which affect specific determinants in the germ which cause that specific part of the head to hypertrophy in the next generation in the special sex corresponding to the germ whose containing soma had its head rubbed. Doubtless there are those who would consider this to be complicated pangenesis worse complicated. There seems to be a further point consistently ignored by adherents to such a theory. They point out that only those animals have horns which fight by butting and believe that this proves that horns are developed by butting. They imply that if horses fought by butting they would develop horns; but it seems rather likely, on the other hand, that if horses had horns they would fight by butting. Cunningham, himself, quotes Rörig to the effect that stags with no antlers guard the females,

not by butting, but by fighting with their fore feet. Likewise Henslow claims that similar structures in widely different plants in similar environments prove that these structures were directly produced by the environment. On the other hand, it can not be denied that some of these cases may be due to the similar selective action of similar environments.

Even Weismann was prepared to admit the inheritance of acquired characters in Protozoa, but Jennings[4] has thrown experimental doubt upon that also. In a second paper[5] he shows that the environment is, indeed, a large factor in determining the size of *Paramecium*, but, as yet, he has found no proof that these effects are inherited. Even selection seems powerless to affect the size within a "pure line." However, pure lines differing in size can easily be isolated by selection, thus confirming by a zoological example the results reached by several botanists, notably Johannsen. The variation curve of size is considered to be formed by a mixture of pure lines whose dimensions are modified by the environment and growth factors.

FRANK E. LUTZ.

EXPERIMENTAL ZOOLOGY

Hybridology and Gynandromorphism.—Raepke [1] has made a detailed examination of some of the hybrids (bastards) between certain species and varieties of Smerinthus (ocellata, populi and its variety Austanti). The material was obtained from the famous hybridologist Standfuss.

The anatomical results may be summed up as follows:

The internal genitalia of the normal male moths show much variation but in the hybrids the variations are more extreme; and often amount to "anomalies," and monstrosities, in the internal organs. Sperm elements are present and reach different stages of maturity, most of them degenerate later, producing a few imperfect spermatozoa. The female hybrids show also greatly modified sexual anomalies, both the germinal region as well as the ducts may be abnormal or even absent. Hand in

[4] "Heredity, Variation and Evolution in Protozoa. I. The Fate of New Structural Characters in Paramecium, with Special Reference to the Question of the Inheritance of Acquired Characters in Protozoa." *Journ. Exp. Zool.*, 5, pp. 577–632, 1908.

[5] "Heredity, Variation and Evolution in Protozoa. II. Heredity and Variation of Size and Form in Paramecium, with Studies of Growth, Environmental Action and Selection." *Proc. American Phil. Soc.*, XLVII, 190, 1908.

[1] Raepke, W. *Jena. Zeitsch. f. Naturwissens.*, XLIV, 1908.

hand with these modifications there appear male secondary sexual characters in the female as more or less rudimentary male genital appendages at the end of the body. It would seem to follow that the female is heterozygous, a fact of some general interest. The discovery raises once more the question of the cause of gynandromorphism in insects, for obviously these hybrid moths show adumbrations at least of such a condition. In this connection it is of interest to give Raepke's summary of Standfuss's results regarding the sex of hybrid moths and the occurrence amongst them of gynandromorphism.

He classifies the results under five headings:

First, those hybrids that are so abnormal (atypic or sexless) that their sex can not be determined.

Second, those hybrids in which only one sex develops, generally the male; females also rarely appear, but these so imperfect that reproduction is impossible. The males also are sterile.

Third, those hybrids in which both sexes appear in normal proportions; the females sterile, the males crossed back to the parent species fertile in various degrees. The offspring of such a union are, however, very abnormal and monstrous both in their primary and in their secondary sexual organs. *In certain series gynandromorphs appear in surprisingly large numbers.*

Fourth, those hybrids in which the females although appearing normal lay either no eggs or abnormal eggs. The males are like those in the last category or like those in the next.

Fifth, those hybrids in which the females produce fertile eggs. These eggs produce only embryos or if the caterpillar stage is reached at all the young are weak. Whenever it has been possible to rear moths by crossing back these females to the parent species (or from the male hybrids of the same cross) only males develop but in such scanty numbers that they have not been tested further.

Whether in the last instance only males are produced because they are hardier than the females or because of some more fundamental relation is not evident from the results.

On the other hand the italicized statement in the third category calls for further examination. What is the cause of the production of so many gynandromorphs?

Two hypotheses have been suggested in recent years along cytological lines that offer at least a formal solution of the problem. Boveri suggested that the entering sperm fuses not with the female pronucleus, but with one of the nuclei derived

from the first division of that pronucleus. Morgan suggested that the result could equally well be "explained" on the assumption of polyspermy—one sperm nucleus fusing with the egg nucleus and the other (or others) producing cells independently of the segmentation nucleus. The gynandromorphs described by Toyama seemed to be a test case. An analysis of his results gave evidence in favor of my suggestion. In connection with the occurrence of two kinds of spermatozoa in moths—"male and female producing"—the question arises whether on my view the male parts of the gynandromorph are due to a male or to a female producing sperm. In my paper I suggested that since the female sperm is the homologue (from the chromosomal point of view) of the egg nucleus minus its two polar bodies that such a "female-producing" sperm might produce the male parts. This suggestion fits in completely with the view of sex-determination recently adopted by Wilson. It sounds paradoxical at first that a "female-producing" sperm could produce a male soma, yet if we look to the chromosomes alone as sex producers such a view is tenable. Moreover if in the bee there is produced only female-producing sperm—as the evidence strongly indicates—then on my view the male parts must come from a female-producing sperm. On Boveri's view the nucleus that makes the male parts is the same (after one division) as the egg-pronucleus which is also male producing and the homologue of the "female-producing" sperm.

T. H. Morgan.

ECHINODERMATA

Red Sea Crinoids.[1]—Mr. Herbert C. Chadwick has just published the first account of the crinoid fauna of the Red Sea, his paper being based upon a collection made by Mr. Cyril Crossland, under the direction of Professor W. A. Herdman, of the University of Liverpool. From time to time notices have appeared relating to various Red Sea comatulids, but they have been widely scattered, and some of them more or less forgotten, so that before the appearance of this paper an idea of the Red Sea crinoids could only be obtained by a most laborious search through a large number of more or less rare and inaccessible volumes.

Mr. Chadwick found six species in the material submitted to

[1] Reports on the Marine Biology of the Sudanese Red Sea.—VII. "The Crinoidea." By Herbert C. Chadwick, A. L. S., Curator of the Port Erin Biological Station. Journ. Linn. Soc. (Zool.), vol. **31**, pp. 44–47.

him, representing only two families, the Himerometridæ and the Antedonidæ, in the former the genera Oligometra, Stephanometra, Dichrometra and Heterometra, and in the latter Iridometra. All of these genera range throughout the East Indian region, and are characteristic littoral types of that area.

The first crinoids known from the Red Sea were *Tropiometra carinata* and *Heterometra savignii*, both of which were well figured by Savigny in his "Description de l'Egypt" in 1817, the former identified by Audouin as "Comatula sp.," the latter as "*Comatula multiradiata.*" There is no further reference to the first of these figures; but de Blainville in 1836 copied the second in the atlas to his "Manuel d'Actinologie"; in doing this he made a curious mistake, for the plate is lettered "*Comatula adeonæ*" though in the text the description of *Comatula adeonæ* is taken from Lamarck, and the species is stated to have ten arms. In the following year the "Penny Encyclopedia" copied de Blainville's account of *Comatula adeonæ*, multiradiate figure and all, and the same slip was made by the "Natural History" of Knight published in 1867.

Rüppel, in the course of his travels, found in the Red Sea an interesting multiradiate comatulid upon which he bestowed the MS. name of *Comatula cucomelas*, but he does not appear to have mentioned it anywhere in his works. In 1833 Leuckart came across his specimens in the Senckenburg Museum, and published the name, together with the locality, though without any diagnosis.

In 1841 Professor Johannes Müller described his *Alecto savignii*, based upon specimens which had been brought from the Red Sea by Hemprieht and Ehrenberg, and he also identified the *Comatula multiradiata* of Audouin, figured by Savigny, as this species. In 1869 von Martens recorded Müller's *Alecto palmata*, which had been originally described from India, from the Red Sea, though he apparently did not know that this was the same form as that recorded as *Comatula leucomelas* by Leuckart in 1833.

Nothing more was recorded regarding Red Sea comatulids for some time; Moseley analyzed the coloring matter from an unidentified species from Suez (possibly *Oligometra serripinna*), and Ludwig in 1880 listed two of the species known from that locality, but omitted the third. Carpenter, in the "Challenger" report was unable to add anything, though he increased the known range of *Heterometra savignii* by recording it from Muscat and

Kurrachee. In 1890 Dr. Hartlaub described *Dichrometra klunzingeri* from Koseir, and identified the *Comatula leucomelas* of Rüppel with the *Alecto palmata* of Professor Müller.

Mr. Chadwick did not find *Tropiometra carinata* nor *Dichrometra klunzingeri* in the collection examined by him, but he did find the other two species known from the Red Sea. *Heterometra savignii* and *Dichrometra palmata;* the remaining four species recorded include one family and three genera new to the region; they are, *Oligometra serripinna*, *Iridometra parvicirra*, *Stephanometra marginata* and *Dichrometra protectus*.

Oligometra serripinna is recorded from Suez Bay, where it was dredged at a depth of 10 fathoms; the specimens differ from the type in the greater number of cirrus joints, and, in view of the general constancy of the cirrus characters in this genus, may eventually turn out to be a recognizable form, as may also those recorded under the same name from Ceylon; correlated, as usual, with the more numerous cirrus joints, the lower pinnules have also more numerous joints.

Iridometra parvicirra, discovered by the "Challenger" among the Philippine Islands, is recorded from ten fathoms in Suez Bay. The single specimen has a large number of cirrus joints for the genus, which, together with the furrowed first primibrach, would suggest that it was rather closer to the *I. nana* group of species than to *I. parvicirra;* the former occur from Mauritius to Japan, while the latter were previously known from the Philippines and Japan.

We share the author's doubt in regard to his identification of *Stephanometra marginata,* which he records from Suez Bay, in ten fathoms.

Dichrometra protectus (under the later name *imparipinna*) is given from Suez Bay, and Suakim. The number of arms in the specimens is unusually small, and it would have been well worth while to have recorded their size. In addition to the localities cited by Mr. Chadwick, the species is known from Cebu, Philippines, Fiji and Singapore.

Dichrometra palmata was found on the coral reef at Misharif Island, Khor Dongola, and from between tide marks at Suez.

Heterometra savignii (emended, following Carpenter, to *savignyi*) is recorded from four fathoms in Suez Bay, from nine fathoms at Ul Shubuk, from ten to twelve fathoms at Khor Shinab, and at the anchorage at Salaka; the distribution of the species is given as "Red Sea, Ceylon," but I am unable to recall any record from the latter place; Carpenter gives it from

as far east as Kurrachee, and says that it "is not known to extend further eastwards," and I know of no subsequent additions to its range; Mr. Chadwick did not give it from Ceylon in his list of the crinoids of that island published in 1904.

In the introductory paragraph Mr. Chadwick mentions the interesting fact that none of the Comasteridæ are known from the Red Sea. They probably occur there, however, and will eventually be discovered when more extended work is undertaken. The absence of any species of Zygometridæ is noteworthy, and also that of Himerometra, one species of which, *H. persica,* was first described from the Persian Gulf and subsequently found in the Philippines. He also takes occasion to point out a weakness in Dr. F. A. Bather's argument for the treatment of a syzygial pair of brachials as two single brachials united by syzygy, instead of a single brachial "with a syzygy," the treatment adopted by Carpenter and Hartlaub. Mr. Chadwick's contention is that if the two brachials united by syzygy were originally, as urged by Dr. Bather, united by the ordinary oblique muscular articulation of the distal portion of the arm, which oblique muscular articulation had been transformed into a syzygy at the same time dropping its pinnule, the pinnule upon the resultant epizygal would be upon the same side as that upon the joint preceding the hypozygal, instead of on the opposite side, as is always the case. Mr. Chadwick is inclined to believe that this is evidence in favor of the views of Hartlaub and Carpenter, and against the ideas of Dr. Bather. I maintain that the syzygial pair is the morphological equivalent, not of one joint, as urged by Carpenter (in part) and Hartlaub, nor of two joints as supposed by Dr. Bather and apparently considered by Professor Perrier, but of *three* joints, the central one of which has dwindled and disappeared, so that the oblique muscular articulations on its proximal and distal ends have become superposed, their ligaments, being dominant over their muscles, fusing and forming the radiating figure which is the original of the later more perfected syzygy, while the muscles, and with them the pinnule sockets (borne by the muscular fossæ) have disappeared. Thus the syzygy originally, instead of having a single pinnule, as supposed by Dr. Bather, had two, which neutralized each other, so that the syzygy in its perfected form has no effect on the pinnulation.

AUSTIN HOBART CLARK.

WASHINGTON, D. C.,
December 7, 1908.

The American Journal of Science

Established by Benjamin Silliman in 1818.

The Leading Scientific Journal in the United States

Devoted to the Physical and Natural Sciences, with special reference to Physics, and Chemistry on the one hand, and to Geology and Mineralogy on the other.

Editor: EDWARD S. DANA.

Associate Editors: Professor GEORGE L. GOODALE, JOHN TROWBRIDGE, W. G. FARLOW and WM. M. DAVIS of Cambridge; Professors A. E. VERRILL, HENRY S. WILLIAMS and L. V. PIRSSON, of New Haven; Professor G. F. BARKER, of Philadelphia; Professor JOSEPH S. AMES, of Baltimore; MR. J. S. DILLER, of Washington.

Two volumes annually, in monthly numbers of about 80 pages each.

This Journal ended its first series of 50 volumes as a quarterly in 1845; its second series of 50 volumes as a two-monthly in 1870; its third series as a monthly ended December, 1895. A Fourth Series commenced in 1896.

Subscription price, $6 per year or 50 cents a number, postage prepaid in the United States; $6.25 to Canada; $6.40 to countries in the Postal Union. Back numbers at reduced prices.

☞Ten-volume Indexes, Vols. I-X, XI-XX, fourth series, price one dollar. Address

The American Journal of Science
New Haven, Conn.

Pour paraître en 1908.

LAMARCK

sa vie, son œuvre

par MARCEL LANDRIEU.

1 vol. gr. in 8° raisin d'environ 550 p. avec un portrait en hèliogravure et renfermant de nombreux documente inédite.

Sera publié dans les Mémoires de la Société Zoologique de France et mis en vente également au prix de **10 fr. Le tirage étant trés limité, prière de souscrire** immédiatement en s'adressant au Secrétaire général,

28 RUE SERPENTE, PARIS.

To Zoologists and Museums

W. F. H Rosenberg

Importer of Exotic Zoological Specimens

57 Haverstock Hill London, N. W. England

Holds the largest stock in the world of specimens in all branches of Zoology.

Just published, my new price list of BIRD'S EGGS, containing over 800 species from all parts of the world. Also price lists Nos. 6, Bird Skins (over 4,300 species), and 7, Mammal Skins, Skeletons, and Spirit Specimens (over 300 species).

Any of the above price lists sent post-free on application.

Science

A weekly journal, established in 1883, devoted to the advancement of the natural and exact sciences, the official organ of the American Association for the Advancement of Science, publishing original articles and notes on the progress of the different branches of science, the proceedings of scientific societies and academies, reviews of scientific books and articles, preliminary accounts of researches and full discussion and news on all subjects concerning scientific men and scientific and educational institutions.

Annual subscription $5.00. Single numbers 15 cents.

The Popular Science Monthly

An illustrated magazine, established in 1872, devoted to the diffusion of science, publishing articles by leading authorities in all departments of pure and applied science, including the applications of science to education and society.

Annual subscription $3.00. Single copies, 30 cents.

The American Naturalist

A monthly journal, established in 1867, devoted to the biological sciences with special reference to the factors of organic evolution.

Annual subscription $4.00. Single numbers, 35 cents.

**** To new subscribers mentioning this advertisement and enclosing one dollar, SCIENCE will be sent for three months, THE AMERICAN NATURALIST for four months or THE POPULAR SCIENCE MONTHLY for six months.*

THE SCIENCE PRESS

Lancaster, Pa.

Garrison, N. Y. **Sub-Station 84, New York.**

The American Naturalist

A Monthly Journal, established in 1867, Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Organic Evolution and Heredity

CONTENTS OF THE OCTOBER NUMBER

The Manifestations of the Principles of Chemical Mechanics in the Living Plant. DR. F. F. BLACKMAN.

The Desiccation of Rotifers. D. D. WHITNEY.

On the Habits and the Pose of the Sauropodous Dinasaurs, especially of Diplodocus. DR. OLIVER P. HAY.

Shorter Articles and Correspondence: Juvenile Substitutes for Smoking Tobacco. Professor WILLIAM ALBERT SETCHELL.

Notes and Literature: *Heredity*—Recent Studies in Human Heredity, DR. F. A. WOODS. *Ornithology*—Riddle on the Cause of the Production of Down and Down-like Structures in the Plumages of Birds, J. A. A. *Vertebrate Paleontology*—New Fossil Mammals from Egypt, T. D. A. C.

CONTENTS OF THE NOVEMBER NUMBER

Further Studies on the Activities of Araneads. Professor THOS. H. MONTGOMERY, Jr.

Notes on the Daily Life and Food of Cambarus Bartonius Bartoni. FLOYD E. CHIDESTER.

Some Points in the Ecology of Recent Crinoids. AUSTIN HOBART CLARK.

Shorter Articles and Correspondence: Evolution without Isolation, O. F. COOK. A Note on the Silverside, JOHN TREADWELL NICHOLS.

Notes and Literature: *Botany*—The Origin of a Land Flora, Professor DOUGLASS HOUGHTON CAMPBELL. *Plant Cytology*—Apogamy in the Ferns, Dr. BRADLEY M. DAVIS. *Experimental Evolution*—Regeneration in Lumbriculus, SERGIUS MORGULIS. *The Budgett Memorial Volume*—John Samuel Budgett, President DAVID STARR JORDAN. *Animal Behavior*—Mind in Animals, Professor H. S. JENNINGS.

CONTENTS OF THE DECEMBER NUMBER

Some Physiological Aspects of Radium Rays. Professor C. STUART GAGER.

On the Origin of Structures in Plants. W. A. CANNON.

Origin and Formation of the Froth in Spittle Insects. BRAXTON H. GUILBEAU.

Shorter Articles and Correspondence: Peculiar Abnormal Teeth in a Jack Rabbit. WILLIAM A. HILTON.

Notes and Literature: *Ichthyology*—Ichthyological Notes, President DAVID STARR JORDAN. *The Inheritance of Sex in Higher Plants*—Digest of Professor C. Correns's Memoir: Professor H. E. JORDAN.

Title Page and Index to Volume XLII.

CONTENTS OF THE JANUARY NUMBER

Juvenile Kelps and the Recapitulation Theory. Professor ROBERT F. GRIGGS.

The Larva and Spat of the Canadian Oyster, Dr. J. STAFFORD.

Shorter Articles and Correspondence: Some Notes on the Traditions of the Natives of Northeastern Siberia about the Mammoth, WALDEMAR JOCHELSON. Age of Trotting Horse Sires, F. R. MARSHALL. The Occurrence of *Batrachoceps attenuatus* and *Autodax lugubris* in Southern California, WILLIAM A. HILTON.

Notes and Literature: *Experimental Evolution*—The Effect of the Environment upon Animals, Dr. FRANK E. LUTZ. *Experimental Zoology*—The Influence of the Size of the Egg and Temperature on the Growth of the Frog, SERGIUS MORGULIS. *Parasitology*—Cestodes of Birds, Professor HENRY B. WARD.

CONTENTS OF THE FEBRUARY NUMBER

Charles Darwin and the Mutation Theory. CHARLES F. COX.

Juvenile Kelps and the Recapitulation Theory. II. Professor ROBERT F. GRIGGS.

Notes and Literature: *Plant Phylogeny*—The Origin of the Archegoniates, Dr. BRADLEY M. DAVIS. *Holothurians*—Clark's The Apodous Holothurians, W. K. FISHER. *Lepidoptera*—The Blue Butterflies of the Genus Celastrina, Professor T. D. A. COCKERELL. *Vertebrate Paleontology*—The Lysorophidæ; Stegocephala; The Cotylosauria: The Oldest Known Reptile: The Age of the Gaskohle; Bison Occidentalis: Nectosaurus: Callibrachion, Dr. ROY L. MOODIE. *Parasitology*—The Sleeping Sickness Bureau, Professor HENRY B. WARD. *Exploration*—Camp-fires on Desert and Lava, Dr. ROY L. MOODIE.

CONTENTS OF MARCH NUMBER

Invitation Papers at the Baltimore Meeting of the Botanical Society of America; Darwin Memorial Session:—Darwin as a Naturalist; Darwin's Work on Cross Pollination in Plants. Professor WILLIAM TRELEASE.

Darwin's Influence upon Plant Geography and Ecology. Professor FREDERIC E. CLEMENTS.

Darwin's Work on Movement in Plants. Professor HERBERT MAULE RICHARDS.

An Examination of Darwin's "Origin of Species" in the Light of Recent Observations and Experiments. Professor EDWIN LINTON.

The Distinction between Development and Heredity in Inbreeding. Dr. EDWARD M. EAST.

Breeding Experiments with Rats. Professor T. H. MORGAN.

Shorter Articles and Discussion: The Chub and the Texas Horn Fly, Dr. ROY L. MOODIE. A New Camel from the Lower Miocene of Nebraska, HAROLD JAMES COOK.

Notes and Literature: *Heredity*—The Chondriosomes as Bearers of the Hereditary Qualities, F. PAYNE. Cultural Bed Mutations in the Potato.

Single Number 35 Cents **Yearly Subscription, $4.00**

The NATURALIST will be sent to new subscribers for four months for One Dollar

THE SCIENCE PRESS

Garrison, N. Y. **Sub-Station 84: NEW YORK** **Lancaster, Pa.**

VOL. XLIII, NO. 509 MAY, 1909

THE AMERICAN NATURALIST

A MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

CONTENTS

		Page
I.	**The Categories of Variation.** Professor S. J. HOLMES	257
II.	**The General Entomological Ecology of the Indian Corn Plant**	295
III.	**Notes and Literatures:** *Biometrics*—Some Recent Studies on Growth. DR. RAYMOND PEARL. *Experimental Zoology*—Cuénot on the Honey-bee, Professor T. H. MORGAN. *The Upholding of Darwin*—Poulton and Plate on Evolution V. L. K.	301

THE SCIENCE PRESS

LANCASTER, PA. GARRISON, N. Y.

NEW YORK: SUB-STATION 84

The American Naturalist

MSS intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS

Lancaster, Pa. Garrison, N. Y.

NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

Important New Scientific Books

PUBLISHED BY THE MACMILLAN COMPANY

Botany

The Origin of a Land Flora. A Theory based upon the facts of Alternation. By F. O. BOWER, Sc.D., F.R.S. With numerous illustrations.

Cloth, gilt top, xi+727 pp., illus., index, 8vo, $5.50 net.

NOTE.—A profound study in the morphology of the lowest forms of plants, with special reference to the development of their reproductive systems. The author endeavors to show that the present land flora has originated from an aquatic ancestor, and traces the methods of specialization to the land habit, and the establishment of the forms of the higher plants. A book of the highest importance not only to botanists but to biologists in general.

NEW AND STANDARD HAND-BOOKS ON AGRICULTURE, ETC.

Elements of Agriculture, Southern and Western. By W. C. WELBORN, B.S., M.S., M.P.A.

Cloth, xvi+329 pp., illus., appendix, glossary, index, 12mo, $.75 net.

NOTE.—This is a thoroughly modern treatise on farming as practiced in the Gulf States, from the point of view of the scientific agriculturist. It is adapted to school use, but is of practical service to any farmer in that part of the country. The author is vice-director of the Texas Experiment Station.

Re-issues of the highly valued Hand-Books known as the Garden Craft and Rural Science Series, edited by L. H. BAILEY, of Cornell University, Editor of "Cyclopedia of American Horticulture," "Cyclopedia of American Agriculture," etc.

The Principles of Fruit Growing. By L. H. BAILEY.
Tenth Edition, $1.50 net, by mail $1.66.

Irrigation and Drainage. By F. H. KING.
Fifth Edition, $1.50 net, by mail $1.68.

Principles of Vegetable Gardening. By L. H. BAILEY.
Sixth Edition, $1.50 net, by mail $1.68.

Bush Fruits. By FRED W. CARD.
Fourth Edition, $1.50 net, by mail $1.66.

Fertilizers. By EDWARD B. VOORHEES.
Tenth Edition, $1.25 net, by mail $1.38

Farm Poultry. By GEO. C. WATSON.
Sixth Edition, $1.25 net, by mail $1.42

Published By **The Macmillan Company** 64-66 5th Ave., New York

THE
AMERICAN NATURALIST

VOL. XLIII *May, 1909* No. 509

THE CATEGORIES OF VARIATION

PROFESSOR S. J. HOLMES

UNIVERSITY OF WISCONSIN

IT is a well-established fact that what are commonly called variations include modifications of quite different import in relation to the process of evolution. Whether or not the variations that are induced in the soma, either by its own activities or through the influences of the environment, have any effect in shaping the course of evolution as they were held to do by Lamarck and his followers, it is evident that they do not count in this process in the same way as variations that arise in the germ. But among the germinal variations themselves there are classes of unequal significance. Variations differ markedly in regard to their stability or permanence. Many variations after their first appearance persist with little modification for an apparently indefinite time. Of these what are commonly called mutations afford conspicuous examples; these are abrupt variations which breed true or nearly so from the start, having their own fluctuating variability, to be sure, but around a mean which does not approach that of the parental type in successive generations. Other variations behave quite differently. They may be selected generation after generation, modifying the stock up to a certain point, after which, if the variety is left to itself, there is revision towards the original parent. It is held by many that these two classes of variations are fundamentally distinct, and that only the first,

so-called discontinuous variations, play an important rôle in the origination of new species.

A considerable proportion of what is described as fluctuating variability is, in many cases, simply somatic variation, having no relation to the germ plasm. It is evident, however, that all fluctuating variability can not be such, otherwise species could not be modified by ordinary methods of continued selection. Our mathematical curves represent two kinds of variability lumped together and which it is in most cases practically impossible to separate. The character of height, for instance, in human beings is to a certain extent an inherited one, but it is determined to a marked degree by influences operating after birth. The usual curves of variation represent both and may even include also variations in the nature of mutations which fail of discrimination from the rest of the aggregate.

De Vries distinguished three kinds of germinal variations, elementary species, retrograde varieties and fluctuations. These three kinds he conceives to be sharply distinguished and produced in different ways. All congenital variability is regarded by him as resting upon qualitative or quantitative changes in the pangens or the organic units of which he conceives living matter to be built up. The pangens form the basis of the unit characters, or independently variable elements of the organism, there being a special kind of pangen for each such character. Variations in the number of pangens cause variations of the fluctuating type which obey Quetelet's law of chance frequency distribution. De Vries maintains and attempts to prove by the citation of several examples that through the selection of such variations modification may be carried to a certain point, but soon a limit is reached beyond which selection is incompetent to effect further improvement. Moreover, continued selection must be practised in order to maintain the condition which has been reached, else the stock will in the course of a few generations revert more or less completely to the ancestral mean.

Retrograde varieties, according to De Vries, are sharply distinguished from fluctuations. They are, as a rule, constant from the start, and differ from the type in only one or at most a very few respects.

They originate for the greater part in a negative way by the apparent loss of some quality and rarely in a positive manner by acquiring a character seen in allied species." "By far the greatest part of the ordinary garden-varieties differ from their species by a single sharp character only. In derivative cases, three or even more such characters may be combined in one variety, for instance, a dwarfed variety of the larkspur may at the same time bear white flowers or even double white flowers, but the individuality of the single characters is not in the least obscured by such combinations.

These varieties, says De Vries, "do not possess anything really new." The loss of a character is merely apparent. "On a closer inquiry we are led to the assumption of a latent or dormant state. The presumably lost characters have not absolutely, or at least not permanently disappeared. They show their presence by some slight indication of the quality they represent, or by occasional reversions. They are not wanting, but only latent." In other words, the only difference between retrograde varieties and the types is the latency or patency of certain characters. The same kinds of pangens are present in the germ plasm of both.

Elementary species, on the other hand,

are distinguished from their nearest allies in almost all organs. There is no prominent distinctive feature between the single forms of *Draba verna*, Helianthemum or of Taraxacum; all characters are almost equally concerned. The elementary species of Draba are characterized, as we have seen, by the forms and the hairiness of the leaves, the number and height of the flower stalks, the breadth and incision of the petals, the forms of the fruits, and so on. Every one of the two hundred forms included in this collective species has its own type, which it is impossible to express by a single term. Their names are chosen arbitrarily. Quite the contrary is the case with most of the varieties, for which one word ordinarily suffices to express the whole difference.

The most important distinction which De Vries draws between retrograde varieties and elementary species is a physiological one. They

behave in quite different manner, when subjected to crossing experiments, and the hope is justified that some day crosses may become the means of deciding, in any given instance, what is to be called species, and what variety on physiological grounds.

When varieties are crossed with the parent type the character that is active in one or the other of the forms will usually be patent in the first generation of offspring. In the second generation there is, according to De Vries, a segregation of characters which takes place in conformity to Mendel's law. Ordinary sugar corn, for example, differs from the usual type in having a part of the starch replaced by sugar in the kernels, which consequently become wrinkled when dry. When these two forms are crossed the active character of starchy kernels is present in all the members of the first generation. In the second generation there is a segregation of these characters, one fourth of the offspring being wrinkled kernels, and three fourths smooth ones. Approximately one third of the latter produce only smooth kernels in subsequent generations, while the other two thirds split up again in the expected Mendelian ratio.

In the crossing of varieties it is possible, according to De Vries, for all the corresponding characters of the two forms to become paired. As the distinguishing feature of the variety is the latency or patency of one or more characters, these characters "will unite as well as though they were both active or both dormant. For essentially they are the same, only differing in their degree of activity. From this we can infer that, in the crossing of varieties, no unpaired remainder is left, all units combining in pairs exactly as in ordinary fertilization." As the varieties differ only in the dominance or latency of certain characters, offspring obtained through crossing them differ only in the same way. For such unions De Vries gives the name "bisexual crosses," inasmuch as there is "complete bisexuality, all unit characters combining in pairs."

In the crossing of the elementary species of Œnothera De Vries found that in the first generation there was a

splitting up of the progeny in various ratios, but that the second and subsequent generations bred true to type, thus presenting a condition just the reverse of Mendelian inheritance. For instance when the mutant *rubrinervis* was crossed with the parent type *Lamarckiana* the first generation of hybrids were either *rubrinervis* or *Lamarckianas*, the proportion varying greatly in different lots. The two kinds of hybrids did not split up in the second generation but bred true to type. Similar results were obtained by crossing several other elementary species of *Lamarckiana* but this kind of behavior does not seem to be generally characteristic of the elementary species of other forms.

In the crossing of elementary species there is, according to De Vries, one unit character which is not mated, since

> the differentiating mark is present in one of the parents and not in the other. While all other units are paired in the hybrid it is not. It meets with no mate and must therefore remain unpaired. The hybrid of two such elementary species is in some way incomplete and unnatural. In the ordinary course of things all individuals derive their qualities from both parents; for each single mark they possess at least two units. Practically but not absolutely equal, these two opponents always work together and give to the offspring a likeness to both parents. No unpaired qualities occur in normal offspring; these constitute the essential features of the hybrids of species and are at the same time the cause of their wide deviations from ordinary rules.

These differences between variations were predicted by De Vries on the basis of his pangen theory, and in his essay on "Intracellular Pangenesis" published in 1889 he expresses the opinion that fluctuating variability which rests upon numerical variation of the pangens plays but a minor part in the modification of species. The "artbildende" or species forming variability, is dependent upon the appearance of an entirely new kind of pangen. When categories of variation are anticipated *a priori* on the basis of a theory of the constitution of living matter there is naturally produced a temptation or bias towards

reading the classification into nature and to the overlooking of transitional stages, and we shall therefore enquire if the distinction which is made between elementary species and varieties is a valid one.

In the first place, there does not seem to be any very good reason why on the pangen theory elementary species should differ in numerous characters from the parent form. A pangen is the basis of a single unit character. Elementary species are produced through the origination of a new kind of pangen. If the becoming latent or dominant of a pangen affects only one unit character of an organism, it is not evident, when a new kind of pangen is produced, why the whole organization of the plant should be so profoundly influenced. Why should not the awakening of a dormant pangen produce as great a change as the production of a new pangen of a somewhat different quality. Says De Vries:

> There can be little doubt but that all the attributes of every new species are derived from one principal change. But why this should affect the foliage in one manner, the flowers in another and the fruits in a third direction, remains obscure. To gain ever so little insight into the nature of these changes, we may best compare the differences of our evening primroses with those between the two hundred elementary species of Draba and other similar instances. In doing so we find the same main feature: the minute differences in nearly all points.

De Vries nowhere gives us a much clearer explanation as to why elementary species and varieties should differ in this way and we must probably be content with referring the matter to different degrees of "correlation."

It is evident that there are allied groups separated by small differences throughout the entire organization, and there are other groups which differ apparently in single characters only, such as the presence or absence of hair, spines or certain colors. Hornless cattle and six-toed cats do not seem to present any general or constitutional differences from the other members of their species, but this is a subject upon which we should exercise great caution, as very slight differences in the rest of the organ-

ization may be correlated with pronounced differences in a single part.

Among the forms arising by mutation from *Œnothera lamarckiana* De Vries distinguishes three varieties, *lævifolia, brevistylis* and *nanella.* These forms are called varieties instead of elementary species because they differ from the type in a few characters only and because of their different behavior when crossed. But even according to De Vries' own description the points of difference are not limited to a single character. *Lævifolia,* for instance, is

> chiefly distinguished from Lamarck's evening primrose by its smooth leaves, as its name indicates. The leaves of the original form show numerous sinuosities in the blades, not at the edge, but anywhere between the veins. The blade shows numbers of convexities on either surface, the whole under surface being undulated in this manner. It lacks the brightness of the ordinary evening-primrose or *Œnothera biennis.* These undulations are lacking or at least very rare on the leaves of the new *lævifolia.* Ordinarily they are wholly wanting, but at times single leaves with slight manifestations of this character may make their appearance. They warn us that the capacity for such sinuosities is not wholly lost, but only lies dormant in the new variety.

The leaves of *lævifolia* are also "a little narrower and more slender than those of the *Lamarckiana.*" But *lævifolia* also shows differences in the flower. "The yellow color is paler and the petals are smoother. Later in the fall, on the weaker side branches these differences increase. The *lævifolia* petals become smaller and are devoid of the emargination at the apex, becoming ovate instead of obcordate."

Brevistylis is characterized by its short style. The stigma is different in shape from that of the parent form; there are differences in the ovaries, and there are only a few seeds produced. These differences may possibly depend upon a single varying character, although

> the leaves of the *O. brevistylis* are more rounded at the tip, but the difference is only pronounced at times slightly in the adult rosettes, but more clearly on the growing summit of the stems and branches. By this character the plants may be discerned among the others, some weeks before the flowers begin to show themselves.

Nanella is a dwarf plant, but it is not distinguished by its smaller size alone.

From its first leaves to the rosette period, and through this to the lengthening stem, the dwarfs are easily distinguished from any other of its congeners. The most remarkable feature is the shape of the leaves. They are broader and shorter, and especially at the base they are broadened in such a way as to become apparently sessile. The stalk is very brittle, and any rough treatment may cause the leaves to break off. . . . The stems are often quite unbranched, or branched only at the base of the spike. Strong secondary stems are a striking attribute of the *Lamarckiana* parent, but they are lacking, or almost so in the dwarfs.

So far as morphological evidence is concerned, the difference between the above forms and elementary species are not so sharp as to inspire one with much confidence in the essential distinctiveness of the two classes. All of these so-called varieties differ in various parts of their organization. It may be said that these differences are dependent through correlation upon the variation of a single character, but if any one maintains that smooth leaves and paler flowers, or small size, brittle stem and short leaf stalks are related in this way, the burden of proof is on his shoulders. If a half dozen characters in different parts of the plant vary it would indeed be difficult, amid a considerable amount of fluctuating variability, to separate on morphological grounds a retrograde variety from a true elementary species, especially since experts are sometimes troubled in distinguishing some of the elementary species from one another. Indeed, De Vries admits that it is often very difficult to decide whether a given form belongs to one or the other of these two groups, but he states that in such cases we have a means of testing the matter experimentally by the formation of crosses. Let us see, therefore, how the test of crossing works out.

In the case of the varieties of *Œnothera lamarckiana* there is in the second generation a splitting according to the Mendelian ratio when the variety is crossed with the parent form, but with varieties of other forms this does

not seem to be an invariable occurrence. Davenport has shown that albinism in poultry is in some cases a non-Mendelian character, and the same is probably true, according to Castle, for the lop-eared condition in rabbits. In the inheritance of long and short hair in guinea pigs there is also a marked departure from Mendelian ratios. In silkworms Kellogg has shown that while most features are Mendelian, cocoon color in some cases follows Mendelian ratios, but in others it proved to be "inconstant as to dominance and recessiveness and numerical proportions, and may even break down and blend." Deafmutism also refuses to come under Mendelian categories according to the statistics compiled by Bell. The foregoing are cases of apparent retrograde variations which form an exception to Mendel's law, but it must be admitted that the majority of such variations which have been investigated show a fair approximation to Mendelian ratios.

In the crosses between the elementary species of *Œnothera lamarckiana* there is commonly a splitting up in the first generation with absence of splitting in the second and subsequent ones. Hybrids of *O. Lamarckiana* and *O. biennis*, however, have nearly the aspect of the latter species and remain true in the second and subsequent generations without reversion or splitting. Crosses between *O. muricata* and *O. hirtella* produced hybrids showing the characters of both parents. These were progagated through four generations and remained "true to this type, showing only slight fluctuations and never reverting or segregating the mixed characters." Instances of constant hybrids between different species are very common and it is unnecessary to specify them here. Such constancy according to De Vries is "one of the best proofs of unisexual unions" or unions between distinct elementary species in which there is always one unpaired pangen.

The attempt to make a general rule for the hybridizing of elementary species leads to many difficulties. In

poultry, as Davenport has pointed out, such characters as pea and rose comb, extra toes and the presence of muffs and beards on the head, are acquisitions which developed since the domestication of the original ancestral species. They certainly can not be regarded as the outcropping of latent characters which are represented in allied forms, but are in the line of progressive variation and therefore according to theory dependent upon the production of new kinds of pangens. any definite rule of inheritance and none of them follow Mendel's law, the extra toes do not seem to come under any definite rule of inheritance, and none of them follow the rule for the hybridization of elementary species.

Consider the forms of the common potato beetle studied by Tower. These arise suddenly, breed true to type and differ from the parent form in many characters, some of which are apparently in the line of progressive evolution. They seem to be as truly elementary species as the mutants of *Œnothera lamarckiana*. Yet when crossed with the parental type they produce hybrids which in most cases give a mixed progeny segregating according to Mendel's law. If we can not call these forms elementary species there is no way of distinguishing such except through breeding experiments, and the distinction De Vries draws between elementary species and varieties amounts to nothing more than the fact that crosses between certain groups follow Mendel's law, while crosses between others do not. There is no correlation between any structural criterion of species and the criterion afforded by breeding experiments.

Now when we attempt to make a classification on the basis of breeding experiments alone we fare little better. With blended inheritance in the first and all subsequent generations, partially blended inheritance, total resemblance of hybrid to one or another parent with or without subsequent splitting, incomplete segregation of characters, splitting of offspring of hybrids in various inconstant and non-Mendelian ratios, and many other irregular

manifestations of heredity, the difficulty of maintaining a sharp distinction between varieties and elementary species on the basis of behavior in inheritance is apparent. Are we to classify a six-toed cat as a variety or an elementary species? The variation is apparently limited to a single character and it has therefore one of the marks of a variety, but the variation is doubtless a progressive one and not due to an awakening of a latent character, and hence possesses one of the features of an elementary species. When crossed some of the offspring of the first generation may inherit the variation and some not, and the same is true for the following generation; but there is apparently no splitting according to the law of Mendel. So far as our knowledge goes the situation is the same in respect to polydactylism in man.

The second volume of the Mutationstheorie, which seems to have been little read by most expositors of De Vries, affords several examples of irregular behavior of the hybrids between elementary species which are very difficult to classify. Crosses between *Œnothera nanella* and *O. rubrinervis*, for instance, the one a retrograde variety of *Lamarckiana* and the other a distinct elementary species, gave very variable results, with splittings in the first and succeeding generations in very inconstant ratios, and the occasional production of blends which bred fairly true. We have here a curious combination of the characteristics of unisexual and bisexual crosses.

It would not be difficult to bring forward many other cases which refuse to fall within the scheme of classification propounded by De Vries. There are many kinds of variations which are inherited in many kinds of ways. The pangen theory of the celebrated botanist has proved a deceptive guide and has led its author to do scant justice to many classes of facts which do not fall in line with it. Hypotheses about paired and unpaired pangens have determined De Vries's classification of the different kinds of variations and profoundly influenced his interpretation of his extensive and valuable researches. The doctrine

of intracellular pangenesis has never received the logical development that characterizes Weismann's theory of the germ plasm and is considerably inferior to the latter as a scholastic production. The explanation it affords of the alleged distinction between varieties and elementary species is, as we have seen, practically no explanation at all. The theory may be consistent with the facts of Mendelian inheritance and the supposed independent variability of parts, but why it should lead one to anticipate that elementary species differing from the parent throughout their organization originate by a single sudden leap is not so clear. Rather it would lead one to expect that organisms would be modified, a part here and a part there, corresponding to the independently variable elements determined by particular pangens, of which there are numerous kinds, until the whole was slowly transformed. De Vries, however, is careful to explain that a single pangen may be responsible for certain characters found in various parts of the organism, such as the color of leaves, flower and fruit, and that pangens are supposed to influence each other's manifestation so that a variation in a single pangen may have a far-reaching effect. In a chapter on the association of characters in his recent book on Plant Breeding a great deal of emphasis is laid upon the value of a study of the correlation of the different parts of the plant. He says:

> We come to the conception of a general interdependency of all parts, organs and qualities of an organism. They are governed more or less by the same laws which cause them to undergo corresponding changes when subjected to the same influences.

It seems to me that the author is here upon treacherous ground. Through the assumption of manifold correlations De Vries attempts to account for a change in a single pangen which has to do primarily with one independently variable part of the organism producing a modification of the organism as a whole, but in so doing he is taking the foundation away from the argument upon which the justification of the pangen assumption rests.

To the extent that the organism is a whole of interdependent parts, to just that extent it gives evidence of not being a piece of mosaic work and hence removes the necessity for a hypothesis of discrete germinal units. De Vries even goes so far as to say that "in order to be correlated the characters must begin by being independent entities which through some later means may come into relation with others." At one time it is argued that the existence of pangens is proved by the fact that the parts of the organism are independently variable; and now it is said that we must assume that pangens must exist to account for the parts being correlated; that is, for the fact that they are not independently variable!

The most salient feature of the mutation theory is that the process of evolution is conceived to take place by sudden steps of considerable magnitude. This has been heralded with *éclat* as enabling us to get rid of certain difficulties inherent in the Darwinian theory, such as the assumed absence of intermediate forms between existing and fossil species and even the contention that the geological history does not afford time enough for the process of evolution as it was formerly conceived to take place. But it is not correct to say that a mutation is necessarily a large variation. Mutations may be very small steps, falling far within the limits of ordinary fluctuating variability, as is especially emphasized by De Vries in his later writings.

In groups (such as brambles, roses, buttercups, willows and many others) where large numbers of species are closely allied, the differences between any two of them become smaller, and the number of distinct forms increasing, the distinction in the end may become reduced to a single differential mark for each two neighboring types. Such differences must be assumed to be produced each by a single mutation.

In the light of experiments made at Svalof, De Vries now concludes that "ordinary varieties of cereals are built up of hundreds of elementary forms which with few exceptions have hitherto escaped observation. The high variability which is commonly attributed to our ordinary

varieties of cereals consists only in the differences among the constituents of the mixtures.'' Much of the improvement of grains that was formerly obtained by continued selection De Vries ascribes to the unconscious selection of elementary species and the gradual improvement of an originally mixed stock. Rimpau's rye, a stable race obtained by gradual selection, is thus accounted for, but the burden of proof is here on the part of the mutationists. It is apparently not so easy to test the rôle of mutations *versus* fluctuations in the improvement of species, because if one should secure a stable race by the usual process of selection, the mutationist might urge that, after all, amid the confusion of seemingly fluctuating variability, there were some mutations which escaped notice, and, through the unconscious selection of these and their offspring, the stock was gradually purified and converted into an improved stable form.

Where ordinary varieties include ''hundreds of elementary forms,'' separated by characters which in many cases are so small that they ''may be scarcely perceptible to the inexperienced eye,'' how is one to tell whether he is dealing with mutations or ordinary fluctuations? The latter may be much greater in extent, and, as we have seen, there is no structural criterion by which a mutation may be recognized. Crossing experiments give us no certain test and we have therefore to fall back upon the criterion of stability and class as mutations those variations which breed true from their first appearance. Here the opportunities for begging the question are excellent. If by the ordinary process of selection a stable race is produced we can of course ascribe it to the unconscious choice of one or more undetected mutations. To be sure, stable races can be produced only on the basis of stable variations, and if this is all that the mutation theory necessarily implies its divergence from Darwin's teaching is not very wide.

If now it should turn out that stability is a matter of degree the last distinguishing feature of the mutation

theory would be destroyed. This is a question upon which we are sadly in need of light. Some of De Vries's own mutations are, however, quite inconstant and show a strong tendency to revert to the parent species. *Œnothera scintillans*, when self-pollinated, produced from 8 per cent. to 52.9 per cent. of *Lamarckianas* and 34 per cent. to 69 per cent. of its own kind and a variable number of other mutants. *O. elliptica* and *O. linearis* repeat their kind in still smaller ratios. The reversion of these mutants like their origin is sudden, but it shows an unstable condition of their germ plasm and it may be questioned if this reversion is essentially different from the slower reversion which often follows the cessation of the selection of ordinary fluctuations.

That the differences between mutations and fluctuations are not so fundamental as the pangen theory implies is indicated by several facts, some of the most suggestive of which have been furnished by De Vries's own experiments. For a number of years De Vries carried on a series of experiments on the corn-marigold *Chrysanthemum segetum*, with the purpose of creating a double-flowered variety. De Vries chose a garden variety of this form, *grandiflorum*, and raised several generations, selecting the seed each time from heads which contained 13 rays florets. After four years of propagation, when he was satisfied of the purity of the isolated strain, De Vries began to discard all plants with less than 21 rays in the terminal head. The selection was continued for a number of generations when a plant appeared which seemed to form a promising one for the production of a double variety.

It was not remarkable for its terminal head, which exhibited the average number of rays of the 21-rayed race. Nor was it distinguished by the average figure for all the heads. It was only selected because it was the one plant which had some secondary heads with one ray more than all the others. This indication was very slight, and could not have been detected save by the counting of the rays of thousands of heads. But the rarity of the anomaly was exactly the indication wanted, and the same deviation would have had no significance what-

ever had it occurred in a group fluctuating symmetrically around the average figure. On the other hand, the observed anomaly was only an indication, and no guarantee of future developments.

From this slight indication De Vries selected for three years more and found that the

average number of rays increased rapidly and with it the maximum of the whole strain. The average came up from 21 to 34. . . . The largest numbers determined in the succeeding generations increased by leaps from 21 to 34 in the first year, and thence to 48 and 66 in the two succeeding summers.

Up to this time, while there was a great increase in the number of ray florets, there was no trace of doubling, but in a few of the best heads "the new character suddenly made its appearance." If sudden, the step was certainly a very modest one. A single plant was found in which careful inspection revealed "three young heads with some few rays in the midst of the disk." "Had the germ of the mutation," asks De Vries, "lain hidden through all this time? Had it been present, though dormant, in the original sample seed? Or had an entirely new creation taken place during my continuous endeavors? Perhaps as their more or less immediate result?" It is stated that "The new variety came into existence at once"—but when? While certain that a mutation must have appeared, De Vries is uncertain when and where it appeared. "The leap," he says, " may have been made by the ancestor of the year 1895, or by the plant of 1899 which showed the first central rays, or *the sport may have been gradually built up during these four years*" (italics mine).

During the next two years improvement by selection was kept up.

The average number of rays which had already risen from 13 to 34 now at once came up to 47 and 55. . . . The maximum numbers came as high as 100 in 1900 and even 200 in 1901. . . . Real atavists or real reversionists are seen no more after the first purification of the race.

A variety which is pronounced "permanent and constant" was produced whose lower limit of the number

of rays was raised to about 34, "a figure never reached by the *grandiflora* parent."

The unbiased reader who has carefully followed the account of the production of this double flower can scarcely escape the feeling that the interpretation of the facts according to the mutation theory is at times somewhat strained. The starting point of the whole process is the selection of fluctuations. Now and then the selection of a somewhat more pronounced variation was made; but the so-called mutations had very small and weak beginnings, and De Vries is uncertain just where they occurred and even suggests that they may have been built up gradually! The selection of fluctuations seems to have had the effect of inducing variations of greater stability, if not greater extent, in the same direction. It is not unreasonable to suppose that the appearance of florets with ligulate corolla on the disk is due to the same factors which cause the increase in the number of ray florets, and the variation may be in reality not so discontinuous as it seems. In fact we are ignorant of the stability or the real discontinuity of many of the steps in advance towards the production of the double flower. If a mutation can make its appearance as an extra ray floret in one case, and by the occurrence of two or three ligulate corollas on the disk of a few flowers of the plant in another, and if both these characters can be increased by selection until they reach a stable condition that is far more highly developed than their original one, the facts do not lend much support to a theory of the saltatory origin of species. Rather they would indicate that species have been formed along lines determined by selective processes much in the same way as Darwin conceived them to be.

By a similar method of selection Burbank has produced a scarlet variety of the California poppy, *Eschscholtzia californica*. He noticed one flower with a fine scarlet line on one petal. From the seed of this plant other poppies with scarlet lines were produced, but only to a slight extent. After selection was practised for some years

a race of pure scarlet poppies was finally obtained with no indication of their yellow ancestor. This case is cited by De Vries as one of mutation, but certainly it required more than one mutation to bring about the result.[1]

Discontinuity may often be more apparent than real, the discontinuous variations in the soma being the outcome of continuous variability instead of abrupt changes in the germ. Let us consider from this point of view the occurrence of digital anomalies such as polydactylism, cleft hand, etc., which are frequently cited as illustrations of discontinuous variability. These anomalies are often strongly inherited, but in most cases which have been fully studied, the inheritance, while partly alternative, is not Mendelian. In the race of polydactylous guinea pigs which Castle has produced and bred for a number of generations the anomaly appeared in different individuals in various stages of completeness. The parent of the group, a male, bore an imperfectly developed toe on his left hind foot. The extra toe contained a claw and probably the phalanges, but it was loosely attached and hung limply down on one side. This male produced 27 young, of which 15 were polydactylous. Of the latter some had an extra digit on both hind feet, others had it on but one, and in a few individuals the digit was more fully developed than in the father. In subsequent generations the anomaly appeared in very different degrees of development, some animals having a fully developed digit, others having a loosely hanging toe with or without a nail, while in extreme cases there was only a fleshy bag of skin without bones or claw which often shriveled up and disappeared a few days after birth. The variation, when appearing on one side alone more frequently was limited to the left side (l. 630, r. 589), and when unequal on the two sides the left one was usually the better developed. Normal and polydactylous individuals did not segregate in Mendelian ratios. In some instances the normal condi-

[1] See also the experiments of MacCurdy and Castle in relation of continuous and discontinuous variation in rats. Publications of the Carnegie Institution, No. 70, 1907.

tion gave evidence of being recessive, but this was not borne out by many other cases in which crosses between normal individuals produced polydactylous young. Crosses of normal individuals both of which were of polydactylous ancestry yielded a much higher per cent. of polydactylous young than did crosses in which one individual came from a normal breed, thus showing a certain tendency in the blood towards polydactylism even when it did not manifest itself by any outward mark. Different males of the same amount of polydactylous ancestry often showed great variation in the potency with which they were able to transmit the anomalous character.

The evidence goes to show that we are dealing here with a tendency which, whatever may be its basis, varies continuously and not abruptly, although producing variations which, taken alone, would naturally be classed as mutations. The extra toe is a new character, but the polydactylous breed behaves neither like an elementary species nor like a retrograde variety. The character fluctuates to the vanishing point and even beyond (as shown by crossing experiments with individuals of different ancestry) and shows varying degrees of fidelity of transmission in different strains. Do we not have a condition intermediate between the abrupt discontinuous variations which breed true with great fidelity and ordinary fluctuations? It might be said that we have to do with a mutation which fluctuates to an unusual degree, although it originally depended upon a sudden change in the germ plasm; but the assertion would have no evidence to rest upon. It might be said, on the other hand, that the variation is dependent on the undue activity of some of the factors of normal development, an expression, for instance of increased growth tendency in the part at a certain period, and that this tendency is kept from definite expression until it reaches a certain strength, when it manifests itself as a sudden variation. This conclusion is warranted, I believe, not only by the great variability

of the anomaly, but by the fact already cited that normal individuals of abnormal ancestry are more apt to produce abnormal offspring than are normal individuals of another strain.

The studies of Lewis and Embleton and of Pearson on the inheritance of split hand and split foot in man yield results in many respects similar to the preceding. Although the normal condition seems to be recessive, segregation does not occur in Mendelian ratios. Often both hands and both feet were abnormal, but frequently not in the same way, and in many cases there were marked differences in the variations on the two sides of the body. As Pearson remarks, it is difficult to specify in such cases what the unit character may be. With this, that or the other bone present in some individuals and absent in others and represented in very varying degrees of development, the inheritance gives little evidence of definite units of any kind. What is inherited appears to be a condition which manifests itself in varying ways and degrees and which can not be accounted for by any theory of the sharp segregation of characters.

Why certain germinal variations are strongly inherited and others not is a problem of much interest, but the solution of it may lie, not in the supposed behavior of distinct morphological entities representing certain parts, but in the physiological relations of the basis of the variation to the organized structure of the germ plasm. The sex cells are organisms as well as the bodies that arise from them; they have the same capacity for self regulation; and it is not at all probable that all kinds of variations that may arise in response to the various influences to which they are subjected should be retained to the same degree. Weismann has made the suggestive comparison between the variations of an organism and the oscillations of a polyhedron on one of the faces upon which it rests. If the oscillations are small the body tends to come to rest in the same situation as before; if they are larger it may topple over upon a new face about which it may oscil-

late as around a new center of equilibrium. Weismann postulates a self-regulating power in the germ plasm which keeps numerous minor fluctuating variations from producing any essential modification of the stock. If, however, a certain variation forms a new center of stability it may be permanent. The various mutants of *Œnothera lamarckiana*,[2] most if not all of which contain the potency of giving rise to any of the others and which present very different degrees of stability, may be due to more or less stable forms which the germ plasm may assume rather than the creation of new kinds of germinal units. The stability of a variation may be due, however, not so much to its extent as the analogy with the polyhedron might lead us to expect as to its kind. Variations which are physiologically congruent with the organized structure of the germ plasm form stable races; those which are not tend to become reduced sooner or later to the norm through the regulatory activity of this substance.

The germ plasm may be conceived to exercise, in regard to its variations, a kind of selective activity which may manifest itself as a proneness of the organism to vary along certain lines. It is well known that there are particular types of variation which crop out independently and more or less frequently and may be faithfully perpetuated. Polydactylism, split-hand and split-foot, albinism and melanism, the appearance of races of hairless animals and glabrous plants, the development of nectarines from peaches and peaches from nectarines, the origin of peloric flowers, etc., have occurred many times in independent

[2] It is of course possible that the mutations of *Œnothera Lamarckiana* result from the impurity of the stock. The species has been for a long time cultivated as an ornamental flower, and we have nothing but conjecture regarding its origin. Should it turn out to be derived from a mixture of two or more forms the mutation theory would be deprived of some of its best evidence, but there would still remain a considerable number of mutations from pure ancestry. In *Œnothera gigas* the interesting fact has been discovered that there is double the normal number of chromosomes. Whether this is the cause or the effect or merely one instance of the differences between this mutant and the type is unknown.

strains. These phenomena may be compared to various anomalies which take their origin in the soma. The embryo in its development is liable to certain accidents resulting in the production of teratological phenomena such as hare-lip, double formations, anencephaly and many others. These anomalies fall into certain classes and in many cases can be attributed to particular defects of development. The germ plasm also may be regarded as liable to certain classes of accidental modifications which produce heritable variations of more or less clearly defined types. No one would think of attributing anomalies of somatic origin to the development of a new kind of organic unit. If the same mutation appears time after time, would it not be more reasonable to suppose that it arose after the fashion of somatic anomalies than that it depended upon the creation each time of the same kind of a new pangen? The fact that mutations can be induced through the influence of the environment certainly favors such a view. Tower found that in Leptinotarsa certain variations or mutations arose repeatedly in independent strains and that by subjecting the beetles to unusual conditions during the period of active development of their germ cells the proportion of these sudden variations could be very greatly increased. The variations thus produced belonged to a few well-marked types, and while it would be hazardous to set bounds to the possible number of mutants the species may produce, it is probable that the number is subjected to a certain limitation imposed by the peculiar organization of the germinal substance.

The selection of variations by the germ plasm may be illustrated by some observations of Jennings upon inheritance in Protozoa. In a few specimens of Paramœcium it was noticed that the body was furnished with a spine-like excrescence. During fission the spine was transmitted to but one of the individuals, the acquired peculiarity not arising on the other. In one case the spine was transmitted through twenty-one generations, when the

strain disappeared. In other cases the spine was gradually diminished during successive divisions and ultimately disappeared. Other anomalies such as crookedness, blunt ends, bent tip of body and various abnormalities, provoked by artificial mutilation, while persisting for a variable number of generations, were eventually regulated out, leaving a normal strain.

In like manner we may imagine that through environmental changes the germ plasm becomes affected by modifications which in the course of a few generations become regulated out, thereby causing a reversion to the primitive stock. Reversion may thus be conceived as but a manifestation of form regulation. Variations to be permanent must be accepted by the organized structure of the germ cells, so that they may be included instead of excluded by the processes of functional equilibration to which these cells like other parts of the organism are continually subjected. The congruity of the variation is the important thing; whether the variation be large or small, sudden or slow, is of much less consequence.

After all, it may be asked, granting that variations may be interpreted in the manner here set forth, do not the phenomena of Mendelian inheritance, showing as they do that characters may be separated and combined in many different ways prove that these characters must be borne by some sort of units in the germ plasm? This is a conclusion which is adopted by a large number of Mendelians, but, plausible as it seems, it is, I believe, a totally erroneous view. In the first place it is open to question if the assumed purity of the gametes is a fact even in typical cases of Mendelian inheritance, but, granting that there is an absolute separation of ancestral tendencies, it by no means follows that there is any sorting of individual unit characters apart from the complex of tendencies which make for the production of the organism as a whole. Hereditary anlagen may perhaps be shuffled and sorted as wholes, but if the germ plasm were composed of discrete parts representing the unit characters

of the individuals, the result would probably be utter confusion instead of orderly development. We might assume that albinism is dependent upon the peculiar properties of a single chromosome, that length of hair is dependent upon the constitution of a second chromosome, that a short tail is associated with a third, and so on. These characters may not be represented by any kind of structural element; they may have their basis in the general chemical constitution of the chromosome and be produced during development in a purely epigenetic fashion. Chromosomes probably have their individual peculiarities of chemical constitution as might be expected from the fact that the chromatin content of an individual represents contributions from many different ancestors. Each chromosome or even a small constituent of the chromosome may have a relation to the inheritance of the whole body, but the peculiarities of one chromatic element may dominate in one part, those of another chromatic element in another. When albinism is eliminated it does not mean that this character alone is separated, but *the anlage of an albino organism*. Even if it is shown that the number of separate characters which Mendelize is greater than the number of chromosomes of the variety, Mendelian phenomena can be explained on the basis of sorting out ancestral tendencies as wholes instead of unit characters. The facts of Mendelian inheritance at present known do not necessarily give any support to the theory of discrete bearers of unit characters, or the theory of the independent variability of parts as conceived by De Vries and Weismann. This is a point which, I believe, needs to be emphasized on account of the uncritical acceptance of these views by so many writers on heredity and variation. The presence or absence of certain characters may be independent of the presence or absence of certain others, but this fact may very readily be accounted for without having recourse to a particulate theory of inheritance.

The mixing up and separation of characters in inheritance, far from proving the independent variability of

parts, is just what renders the proof of this theory exceedingly difficult. The alleged independent variability of parts is Weismann's strongest proof of his doctrine of determinants. If a pit in the ear or a white tuft of hair on the head can be transmitted for several generations without involving any other change in the organism, we are forced to assume, according to Weismann, that there is a small part of the germ plasm varying independently of the rest which forms the basis or determinant of this character. But the contention particularly difficult of proof is that the characters really do appear in independence of the other parts of the organism. A variation may conceivably depend upon a general change in the constitution of the substance of heredity, although manifesting itself most conspicuously in a single part. A pit in the ear may be the most obvious sign of the very slight constitutional differences between two individuals. It is common to find two closely allied species or varieties differing markedly in one or two features and much less conspicuously in numerous other parts of their structure. Peculiarities of horns are sometimes associated with less noticeable characteristics of the hair, thus pointing to a common origin of these features in some general modification of the ectoderm which in turn may result from some change affecting the germ plasm as a whole. Albinism which is so often cited as a unit character is a peculiarity of far reaching correlations, being often associated with impaired sight or hearing, diminished fertility, and even lessened power of resistance to disease.

To establish the independent variability of parts requires a much closer study of possible correlations than has yet been made. The task is rendered particularly difficult by the varied combination and segregation of ancestral tendencies, which we have just considered. If we can account for the independence of certain characters on the ground of combining and sorting ancestral tendencies as wholes, one has to disprove the possibility of applying this explanation of the appearance of a partic-

ular variation before the latter can be regarded as giving evidence of a corresponding determinant. The burden of proof is on the shoulders of the upholders of the doctrine of determinants and it is a far heavier one than the champions of this doctrine commonly appreciate. Let us suppose that among the various sets of hereditary tendencies that find expression in the organization of an individual one should include the production of a particular variation in a single small part. The constitutional differences which may go along with this peculiarity and of which it may be regarded as one expression may be modified or kept from becoming manifest by other and rival sets of hereditary tendencies thereby rendering it almost impossible to detect the correlations that really exist, and giving the character the delusive appearance of independence. The question of the independent variability of parts is a crucial one for the particulate theories of inheritance, but it is one so beset with practical difficulties that a final answer may not soon be forthcoming.

In the preceding discussion the attempt has been made to show that the various categories of variations recognized by De Vries and others are not sharply separable either on morphological grounds or by their behavior when subjected to crossing experiments. The attempt was made also to show that neither the facts of variability nor those of Mendelian inheritance give any support to the doctrine of pangens, determinants, or other assumed bearers of unit characters, and that unit characters, as elements than can enter or depart from the complex of tendencies that make up an organism probably have no existence. It is evident that variations differ in their stability, but the explanation of this fact may lie in the physiological relations of the variation rather than in some hypothetical representative unit. Whether the variations of the discontinuous type have been influential, in any marked degree, in shaping the course of evolution is a question upon which we need much more evidence. Mutations, as we have seen, may be very small affairs.

About the only criterion by which they may be recognized is their stability, and even that gives some evidence of being a matter of degree. No limit has been discovered to the minuteness of the stable modifications that may occur, and it may happen that further study will reveal the comparatively frequent appearance of very slight variations of this kind. In fact, considerable progress has even now been made in this direction by the study of grains; and the number of more or less stable modifications that are likely to be discovered threatens to overwhelm systematists with the labor of naming and describing them. In many organisms not propagated by self-fertilization the detection of these small steps is no easy task and the attempt to describe them all would undoubtedly prove a futile effort. Among human beings, for instance, what are we to designate as elementary species? We meet with all grades of differences from well-marked family traits to those which separate the Caucasian from the negro. Are we to regard the Hapsburg lip which was transmitted with fidelity for many generations as the mark of an elementary species? It was apparently a new character and therefore presumably dependent upon a new pangen or determinant. The Celts, Teutons, Slavs, etc., differ by more or less constant characters which are constitutional and not confined to single parts, and the same may be said of the various subdivisions of these groups. The Aryan stock to which these groups belong is separated by still greater differences from the other subdivisions of the Caucasian race, and the latter in turn differs still more widely from the negroes and Mongolians. One has considerable difficulty in disposing of these groups either as varieties or elementary species. They can not from De Vries standpoint be considered the results of fluctuating variability on account of their constancy even under very varied external conditions. If the small divisions have arisen by slow changes, as everything indicates, there is no logical halting place short of admitting that the greater ones may have done

the same. In fact a survey of the racial differences of man in their varying degrees and kinds and their correlation with geographical distribution shows us pretty clearly that these differences have been slowly acquired by the summation of very small variations. These groups are not related as the so-called retrograde or digressive varieties are, but they are based on differences in general constitution affecting the shape of the skull, the characteristic complexion, the general temperament, and many other traits too numerous to specify. They may have arisen by minute, discrete, stable variations, but to call each step in advance an elementary species seems absurd, and to talk of the immutability of species still more so. We gain little by characterizing as elementary species the small steps of which there may be a dozen or more separating a German from a Frenchman.

Students of geographical distribution as a rule set little store by the theory of mutation. The relation of variation and species-forming to distribution as illustrated by the work of Gulick and Hyatt on the Achatinellidæ, the Sarasins on the snail fauna of Celebes, of Plate on the mollusca of the Bahamas, and of many students of the mammals, birds and fishes of North America indicate that the steps concerned in species-forming have been very modest ones. If sudden mutations of considerable magnitude have been a not uncommon source of varieties of domesticated animals and cultivated plants it does not follow that the selection of comparatively small variations has not been the predominant method of species-forming in a state of nature.

After fifty years from the publication of Darwin's "Origin of Species" we are still debating, and more lively than ever, the central problem of that epoch-making book; but it is not improbable the views of its sagacious author will prove more nearly correct than those of most of his modern critics. Much remains to be done before the problem is finally solved, and there are few fields

before the investigator that are more fruitful and alluring.[3]

[3] *Mendelism and Unit Characters.*—Since this article on the Categories of Variation was sent in for publication several articles have appeared whose contents would have been referred to had they been published somewhat earlier. One of these is a short paper by W. J. Spillman in "The Nature of Unit Characters," in the April number of this journal, in which an interpretation of so-called unit characters is given which is, in many respects, similar to my own. Reference to Mr. Spillman's views would naturally be expected in an article appearing later than his in the same journal, so that it may be well to state that the proof of my paper was returned to the publishers in the first part of February, and that no modification of the paper has since been made. I am glad to find myself in agreement with Mr. Spillman at least to the extent that the facts of Mendelian inheritance do not compel us to adopt a particulate theory of heredity. That Mendelian inheritance can be explained by the sorting process which is supposed to take place in the reducing divisions of the germ cells I feel by no means assured, there are grave difficulties in the way of such an interpretation. But if this explanation prove to be the correct one it would be far from justifying the commonly accepted doctrine of unit characters with all its evolutionary implications.

Reference might also be made to some recent articles by De Vries, especially one on the crosses of *Oenothera nanella* (Ueber die Swillingsbastarde von *Oenothera nanella*. Ber. Bot. Ges. 26, p. 667, '08), inasmuch as the experiments reported tend to strengthen further the contention of the present writer that no sharp line can be drawn from the results of crossing experiments between elementary species and so-called retrograde varieties.

THE GENERAL ENTOMOLOGICAL ECOLOGY OF THE INDIAN CORN PLANT

PROFESSOR S. A. FORBES

ILLINOIS STATE ENTOMOLOGIST

ECOLOGY being the science of the interactions between an organism, or a group of organisms, and its environment, and between organisms in general and their environment in general, this complex of relations may, of course, be divided in various ways. The division here used implies a centripetal grouping of the facts of relationship around single kinds of organisms, and the group of facts to be discussed is that of which the corn plant is the center and the insects of its environment are the active factors.

A prolonged study, extending over many years, of the entomology of the corn plant, the economic results of which have been published in my seventh and twelfth reports as State Entomologist of Illinois (the Eighteenth and Twenty-third of the office series) has left in my possession a considerable body of information capable of treatment from the standpoint of pure ecology, and the beginnings of such a treatment are here assembled because of the rising interest in ecological investigation and the promise which it gives of interesting and important results, and because of a wish to illustrate, in some measure, the general scientific value of such materials, of which, it scarcely need be said, the economic entomologists of this country have accumulated a large amount.

INSECT INFESTATION OF THE CORN PLANT

We know of some two hundred and twenty-five species of insects in the United States which are evidently attracted to the corn plant because of some benefit or advantage which they are able to derive from it. The

principal groups of this series are ninety species of Coleoptera, fifty-six species of larvæ of Lepidoptera, forty-five species of Hemiptera and twenty-five species of Orthoptera. The other insect orders are represented by seven or eight species of Diptera and one or two of Hymenoptera. Every part of the plant is liable to infestation by these insects, but the leaves and the roots yield the principal supplies of insect food, either in the form of sap and protoplasm sucked from their substance by Hemiptera, or in that of tissues and cells devoured by the subterranean larvæ of Coleoptera, and by caterpillars, grasshoppers and beetles, feeding above ground.

Lack of Special Adaptations

Notwithstanding the great number of these insects, and the variety and importance of the injuries which they frequently inflict upon the corn plant, there is little in its structure or its life history to suggest any special adaptation of the plant to its insect visitants—no lure to insects capable of service to it, or special apparatus of defense against those able to injure it. The fertilization of its seed is fully provided for without reference to the agency of insects. It has no armature of spines or bristly hairs to embarrass their movements over its surface or to defend against their attack its softer and more succulent foliage. It secretes no viscid fluids to entangle them, and forms no chemical poisons or distasteful compounds in its tissues to destroy or to repel them. The cuticle of its leaf is neither hardened nor thickened by special deposits; its anthers are neither protected nor concealed; and its delicate styles are as fully exposed as if they were the least essential of its organs. Minute sucking insects are able at all times to pierce its roots and its leaves with their flexible beaks, and with the single exception of its fruit there is no part of it which is not freely accessible at any time to any hungry enemy. Only the kernel, which is supposed to have been lightly covered in the wild corn plant by a single chaffy scale or glume, has

become, in the long course of development, securely inclosed beneath a thick coat of husks, impenetrable by nearly all insects; and we may perhaps reasonably infer that, among the possible injuries against which this conspicuous protective structure defends the soft young kernel, those of insects are to be taken into account.

There are, of course, many insect species, even among those which habitually frequent the plant, which are unable to appropriate certain parts of its substance to their use, but this is because of the absence of adaptation on their part and not because of any special defensive adaptation on the side of the plant. Thus we may say that, with the exception of the ear, the whole plant lies open and free to insect depredation, and that it is able to maintain itself in the midst of its entomological dependents only by virtue of its unusual power of vigorous, rapid and superabundant growth. Like every other plant which is normally subject to a regular drain upon its substance from insect injury, it must grow a surplus necessary for no other purpose than to appease its enemies; and this, in a favorable season, the corn plant does with an energetic profusion unexampled among our cultivated plants. Insects, indeed, grow rapidly as a rule, and most of them soon reach their full size. Many species multiply with great rapidity, but even these the corn plant will outgrow, if given a fair chance, provided they are limited to corn itself for food.

Turning to the other side of the relationship, we may say that the corn insects exhibit no structural adaptations to their life on the corn plant—no structures, that is to say, which fit them any better to live and feed on corn than on any one of many other kinds of vegetation. This was, of course, to be expected of the great list of insects which find in corn only one element of a various food, and that not necessarily the most important; but it seems equally true of those which, like the corn root-worm or the corn root-aphis, live on it by strong preference, if not by absolute necessity.

Aphis maidiradicis, the so-called corn root-aphis, is not especially different in adaptive characters from the other root-lice generally, and it lives, indeed, in early spring, on plants extremely unlike corn. Finding its first food on smartweed (Polygonum), and on the field grasses (Setaria, Panicum, etc.), it is scarcely more than a piece of good fortune for it and for its attendant ants if the ground in which it hatches is sometimes planted to corn, in which it finds a more sustained and generous food-supply than in the comparatively small, dry and slow-growing plants to which it would otherwise be restricted.

The larva of *Diabrotica longicornis*, usually known as the corn root-worm, is, of course, well constructed to burrow young corn roots, but it differs from related Diabrotica larvæ in no way that I know of to suggest a special adaptation to this operation, except in the mere matter of size. If it were larger it would probably eat the roots entire, as does the closely related and very similar larva of *D. 12-punctata*. Indeed, there is some reason to believe that *D. longicornis* may breed in large swamp grasses, since the beetle has been found abundant in New Brunswick in situations where it is difficult to suppose that it originated in fields of corn, and where such grasses are extremely common. Even the special corn insects seem, in short, structurally adapted to much more general conditions than those supplied by the corn plant alone, and if they are restricted largely or wholly to this plant for food, this seems due to other conditions than those supplied by special structural adaptations.

In short, in the entomological ecology of the corn plant we see nothing whatever of that nice fitting of one thing to another, specialization answering to specialization, either on the insect side or on that of the plant, which we sometimes find illustrated in the relations of plants and insects. The system of relations existing in the corn field seems simple, general and primitive, on the whole, like that which doubtless originally obtained between plants in general and insects in general in the early stages of their association.

Such adaptations to corn as we get glimpses of are almost without exception adaptations to considerable groups of food plants, in which corn is included—some of these groups select and definite, like the families of the grasses and the sedges, to which the chinch-bug is strictly limited, and others large and vague, like the almost unlimited food resources of the larvæ of Lachnosterna and Cyclocephala under ground. These are evidently adaptations established without any reference to corn as a food plant, most of them very likely long before it became an inhabitant of our region, and applying to corn simply because of its resemblance, as food for insects, to certain groups of plants already native here.

ENTOMOLOGICAL ECOLOGY OF CORN AND THE STRAWBERRY

Corn being, in fact, an exotic or intrusive plant which seems to have brought none—or at most but one[1]—of its native insects with it into its new environment, it will be profitable to compare the entomological ecology of this introduced but long-established and widely cultivated plant with that of some native species which is also generally and, in some districts, extensively grown.

We may take, for this purpose, the strawberry plant, whose insect visitants and injuries I studied carefully several years ago. About fifty insects species are now listed as injurious to the strawberry, and about twenty of these also infest corn. Two fifths of the known strawberry insects are thus so little specialized to that food that they feed on other plants as widely removed from the strawberry as is Indian corn. On the other hand, six species, all native, are found, so far as known, only, or almost wholly, on the strawberry, at least in that stage in which they are most injurious to that plant. These are the strawberry slug (*Emphytus maculatus*); the strawberry leaf-roller (*Phoxopteris comptana*)—occasionally abundant on blackberry and raspberry, to which it spreads from infested strawberry plants adjacent; two

[1] ***Diabrotica longicornis* Say.**

of the strawberry root-worms—the larvæ of *Typophorus aterrimus* and of *Scelodonta nebulosus*; the strawberry crown-borer (*Tyloderma fragariæ*); and the strawberry aphis (*Aphis forbesi*).

Not even one of this considerable list exhibits, so far as I can see, any special structural adaptation to life on the *strawberry* plant. The two root-worms mentioned, for example, are no better fitted to feed on strawberry roots than is a third strawberry root-worm—the larva of *Colaspis brunnea*, which lives on the roots of corn and timothy also. *Emphytus maculatus* might feed, for all the structural peculiarities which one can see, on the leaves of roses as well as does the common slug or false-worm of those shrubs—and so of the others of the list. Even the strawberry crown-borer, which lives in all stages solely on that plant, might, so far as structure and life history are concerned, feed and develop in any other thick-rooted perennial. The difference seems to be one of habit or preference solely, and not of structural adaptation.

Our impressions of the extent, nicety and frequency with which insects and plants are mutually adapted are indeed commonly much exaggerated, owing to the fact that our attention is especially drawn to notable cases of curious, precise or particularly advantageous adjustments between organisms, while no general study is made of the entire system of relations obtaining between all the members of an associate group, varying widely, as these do, in respect to the intimacy, importance and exclusiveness of the association. For this same reason, in part, we ordinarily have no accurate idea of the relative frequency and primacy of structural, or static, adaptations—particularly obvious, especially interesting, and seemingly ingenious, as they often are—and of those more obscure adaptations of preference, behavior, habit and the like, which, taken together, we may call dynamic.

CLASSIFICATION OF ADAPTATIONS TO FOOD

A plant-insect group—a group, that is, composed of a plant and its insect visitants—is not, in fact, usually marked, either as a whole or in any of its several parts, by the presence of adaptive structures special to that group. The structural adaptations of insects are, as a rule, much too broadly shaped to fit them closely to any one plant, and where such a fitting is found, it is clearly due to some other than the structural factor. Such facts bring us to a consideration of the whole subject of the variations and classification of the adaptations of insects to their food resources.

These adaptations may be classed as structural, physiological, psychological, synethic,[2] local, biographical and numerical. All structural adaptations are, of course, physiological, in a sense, but I use the word physiological, as a matter of convenience, for functional adaptations not based on obvious structural peculiarities, as where an insect equally capable of feeding on the sap of two plants, and readily availing itself of either, nevertheless thrives and multiplies better on one than on the other, the adaptation being evidently digestive or assimilative rather than obviously structural. The San José scale, for example, feeds readily on a great variety of trees and shrubs, on some of which it thrives poorly and spreads but little, while on others it multiplies enormously and spreads with great rapidity. The word psychological may be applied to cases of apparent choice or evident inclination, as between the various available food plants of the environment. Those fixed peculiarities of habit or behavior which adapt an insect to one food plant or class of food plants rather than to another we may call synethic adaptations, in the absence of any existing word applicable in this sense; local adaptations are those in which the usual haunts and places of resort of an insect species, however determined, bring it into common contact with an available food plant, the frequency of this

[2] Adaptations of habit.

contact being quite independent of the degree of the fitness of such plant for its food; biographical adaptations are those based on a correspondence between the life history of the insect and its organic food supply, such that the latter shall always be accessible in sufficient quantity to meet the varying needs of the dependent insect at the various stages of its growth; and numerical adaptations are the consequence of such an adjustment of the rate of insect multiplication to the plants or animals of its food that only the unessential surplus of this food shall be appropriated, leaving its essential maximum product undiminished.

These several classes of adaptations limit each other variously, the most desirable food of an insect being that which is found within the area common to all of them. That is, the most important food plants of a vegetarian species will be those which are well within its structural capacities of discovery, access and appropriation; within its physiological powers of easy digestion and profitable assimilation; and within its habitual range and location; and which are consistent with its usual preferences and habits of action, and are well adapted to furnish continuously amounts of food answering to its varying necessities during the different stages of its life.

Advantages of Biographical Adaptation

It is obviously to the advantage of any insect species that it shall have its largest possible food supply coincident with its own largest demand for food—that is, at the climax of its period of growth. In a species restricted to one annual food plant the most favorable relation will usually be that in which the life history of the plant and that of the insect coincide, the egg-laying period of the one corresponding to the seeding period of the other, the hatching of the insect being virtually simultaneous with the germinating period of the plant, and the period of most rapid growth being coincident in both. This kind of adaptation is well illustrated by the life histories of

Diabrotica longicornis and the corn plant. This beetle lays its eggs in fall when the ear is maturing, and the larvæ hatch in spring when the corn plant is young and growing slowly, and they feed on the roots during the entire growing season of the plant. It is evident that such a well-adjusted insect will have an advantage, other things being equal, over a poorly adjusted competitor for food from the same plant, since it will be able, as a rule, to leave a more vigorous and abundant progeny; and similarly, any part of a species which, by aberration of life history, may come to be poorly adjusted to its food plant, will suffer as a consequence in comparison with the normal members of the species, with the result that these biographical characters of the insect will tend to become permanent and characteristic in the same sense in which its structural characters are.

It should be noticed, also, that such an adjustment is an advantage to the host plant as well as to the dependent insect, since it distributes the depredations of the latter in a way to make them relatively slight when but little injury can be borne, and concentrates them, on the other hand, where the largest injury can be supported with the least serious consequences. Such a well-adjusted insect will get the maximum amount of food with the minimum injury to the plant, and such a plant-insect pair will have a competitive advantage over a poorly adjusted pair in which a greater injury is done to the plant than is necessary to the maintenance of the insect.

The same reasoning applies, and the same rule holds good, for species with a more heterogeneous food, except that in respect to them we must substitute for the single plant the entire group of plants to which the insect resorts for food. At this point, however, the facts become too complicated for successful analysis, especially in view of the difference of abundance from year to year of the plants of a considerable list, and the effects, on the food supply, of variable competitions among the various species resorting to it. It may be said, in general terms, how-

ever, that when the life history of a food plant, or the common history of a group of such plants, exhibits sufficiently constant characters to serve as an adaptive matrix, an adaptation to it of the life history of those insects strictly or mainly dependent on it for food is more or less likely to follow.

Mutual Biographical Adjustments of Competitors

An example of the competitive relations into which corn insects of widely different character, origin, habit and life history may be brought by their dependence on the same food plant may be found in *Diabrotica longicornis* and *Aphis maidiradicis*. Both pass the winter as eggs in the earth of the corn field, the aphis hatching sooner than the root-worm, and developing two or more of its short-lived generations before the Diabrotica larva is out of the egg, gaining thus the advantage of an earlier attack in greater numbers. It is also able to take much more rapid possession of a field of corn because of its command of the services of ants in finding its way to the roots of the plants which the tiny and feeble Diabrotica larva must search out for itself.

Later the root-aphis gives origin to young, many of which acquire wings and may thus disperse as their local attack upon the plant becomes unduly heavy, while the root-worm must take its chances for the year in the field where the eggs were left the previous fall. The aphis feeds at first on the sap of young weeds common in spring in all cultivated fields, and may thus save itself even though the ground is planted to wheat or oats, an event which causes the death by starvation of every root-worm hatching from the egg.

In respect to rate of multiplication, the root-aphis has, of course, a truly enormous advantage as compared with the corn root-worm, and yet, notwithstanding all these facts favorable to the aphis, its injuries to corn in Illinois are seemingly no greater than those done by the corn root-worm. This is due partly to the fact that, through

the winged members of the early generations, the percentage of which increases as conditions become locally less favorable, the aphis largely leaves the field in which it originally started, and early breaks the force of its attack by a general distribution of it. The depredations of the root-worm, on the other hand, increase with the growth of the insect until about September first, and increase also, at a rapid rate, from year to year in a field kept continuously in corn. It follows, as a consequence, that the principal damage by *Aphis maidiradicis* is done to the corn while it is young, and that by Diabrotica to the well-grown plant.

This serial order of injuries to the corn plant, due to the relation of the life histories and rates of multiplication of these two competing insects, is an advantage to both of them, and, indeed, to all three, corn included, since the plant would be more seriously injured or more certainly destroyed if both its insect enemies attacked it together than it is where their attacks are made successively. Competitors for food from a living plant find it to their advantage, and to that of the plant they feed upon, to avoid a simultaneous competition; and such a plant-insect group would, of course, prevail, other things being equal, over a competing group not so adjusted. Natural selection tends, no doubt, to establish these mutually advantageous relations between a plant and its constant insect visitants. With respect to these two corn insects, however, it must be admitted that no proof is apparent that such adaptation of life histories and habits as we here see is due to anything more than an accidental collocation of species whose significant peculiarities were already established when they came together.

A similar but more striking example of a serial succession of injuries to the same plant is to be found among the strawberry insects, as I showed several years ago.[3] Three coleopterous larvæ belonging to the same family

[3] "On the Life Histories and Immature Stages of Three Eumolpini," *Psyche*, Vol. 4, Nos. 117–118, January–February, 1884; and No. 121, May, 1884.

(Chrysomelidæ) but to different genera (Colaspis, Graphops and Typophorus), and to species native in the United States, are all so closely adapted to underground life and to the root-feeding habit that they are distinguishable from one another only by rather slight and inconspicuous characters. They are often associated in large numbers in the same fields, living wholly on the roots of strawberry plants, which they affect in an identical manner, so that from the appearance of the injury itself one could not possibly tell which of the three species was present in the field. One of these root-worms, the Colaspis larva, feeds also on the roots of other plants, especially on those of timothy and corn, but the two other larvæ have been found only among strawberry roots. They seem thus to be strict competitors for food from the same part of the same plant, and as their locomotive capacity is poor, they are unable to avoid one another's company by migration under ground.

The strawberry plant, however, grows continuously throughout the season, and each of these three insects, having a short larval period, feeds on strawberry roots for only a part of this growing season. It is an interesting and striking fact that the life histories of the three competing insects are so related that the larvæ do not infest the plant at the same time, but follow one another in close succession, beginning early in May and ending late in the fall. The first of the species, the Colaspis larva, feeds from about May, to the end of June, the Typophorus larva follows in July and August, and the Graphops larva begins in August and continues until fall.

Consistently with this difference, the species concerned hibernate in different stages of development—Colaspis apparently as an egg, Typophorus undoubtedly as an adult, and Graphops as a larva in its subterranean cell, from which adults emerge the following June to lay their eggs in July. With such a distribution of their attack, each of these three species is able to maintain itself on the strawberry in numbers as large as would be possible for

all three taken together if they made their assault on the plant simultaneously. The advantage to both plant and insects of this adjustment of life histories—if one may call it such—is obvious at once.

That some actual adjustment of larval periods has here been made is rendered somewhat more probable by the fact that a closely related species of Graphops which infests the wild primrose (*Œnothera biennis*) in southern Illinois, has a life history different from that of the species which breeds in the strawberry—hibernating as an adult, like Typophorus, and not as a larva, like the strawberry species of its own genus.

MALADJUSTMENT OF COMPETITIONS

The corn plant is in greater danger from insect ravage during the first month of its life than at any later time. This is because it offers then a comparatively scanty supply of food, so that a small number of insects may work great destruction; because the single small plant is much more easily killed than a larger one; and because a larger number of active rival insects infest corn when it is young than at any other time, some of them beginning with the recently planted or just sprouting seed. The young roots, the underground part of the stalk, the stalk above ground, and the leaves, both before and after they unfold, are all liable to infestation by several species at the same time. The seed is injured by the wireworms, the seed-maggot, the Sciara larva and the larva of *Systena blanda*; the roots, by the wireworms, the root-aphis, the corn root-worms, and the white-grubs; the stalk under ground, by the wireworms, the root-aphis, the southern corn root-worm, and the bill-bugs; the stalk above ground, by the bill-bugs, the cutworms, the web-worms, the stalk-borers, and the army-worm—sometimes by the chinch-bug also; and the leaves, by the bill-bugs, the web-worms, the cutworms, the army-worm and the first generation of the ear-worm.

This concentration of injury upon the corn when it is

young is a case of maladaptation, since the plant has least to offer when it is most heavily drawn upon. It will be noticed, however, that this early spring attack is mainly delivered by insects which come into corn from some other vegetation, chiefly from grass, and whose occurrence in the corn field is scarcely more than accidental. The motive to an adjustment of habits and life histories to the capacities of the plant is therefore virtually wanting, and seems at any rate impossible, owing to the variability and inconstancy of the several factors involved.

Conclusion

From the foregoing it will be seen that the corn plant is not only an exotic in its origin, but that, aside from its relation to man, it still remains an unnaturalized foreigner, not sufficiently adapted to our conditions to survive without the constant supervision of a guardian and the services of a nurse. The corn field contains an artificial "association" persistently maintained by human agency in the midst of a hostile environment, to which it would promptly succumb if left to itself, and as such it would seem to offer to the ecologist all the advantages of a vast and long-continued experiment, by a study of whose results he may learn something of the manner in which ecological relations may be affected when a plant takes advantage of a single favoring condition to push its way into a territory foreign to its former habits.

This corn plant, at least, which has certainly lived in our territory under the care of man for several centuries, and perhaps for some millenniums, has even yet no specialized friends active in its service, and no structurally adapted enemies enlisted against it, such specializations of injurious relationship as one detects being clearly due to other than structural differentiations. During all this long period, it has been widely and steadily forced into a strange ecological system which has nevertheless scarcely yielded to it at any point. It has produced, it is true, by its enormous multiplication and

extension, a profound effect on the numbers and distribution of some insect species, reducing the area of multiplication for several, which, like the cutworms and the army-worm, formerly bred in the turf of our native prairies, but can not breed in fields of corn; and immensely extending the range and increasing the number of others which have found in this plant a better and far more abundant food supply than that originally available to them. Insect species which, like *Diabrotica longicornis* and *Aphis maidiradicis*, were almost unknown fifty years ago within our territory, have now, through their increase in cornfields, arisen to the rank of dominant species.

But the few discernible insect adaptations to the offerings of the corn plant are physiological, psychological, synethic and biographical, and apparently not structural at all. Slight and seemingly incipient as they are, we have no sufficient reason to conclude that they are recent results of the association of the corn plant with the insect; both parties of the association may have been substantially what they now are when they first found each other, and such mutual fitness as they exhibit may be merely like that of angular stones shaken together in a box until like surfaces seem to cohere, simply because in this position the fragments can not readily be shaken apart.

We may also derive, from this discussion, support for the idea that adaptations of insects to their environment are largely, and often primarily, psychological—that they are often, in the first instance, specializations of preference or choice, or, as we may perhaps more safely say, of tropic reaction. Species which would otherwise compete with each other, with disadvantageous consequences to each, escape these disadvantages by acquiring, one or both, different habits of reaction, under the influence of which they separate, one going for its principal food to the corn plant, for example, and the other continuing on the strawberry, although structurally each remains equally fit to feed on either. Physiological, or even struc-

tural, adaptation may follow the psychological, but as secondary to it. This is only saying in other words that the central nervous system, on which special functioning peculiarities of habit depend, is subject, like any other, to adaptive variations, and that these variations may either follow and reinforce those of some other organ or organs tending to the same end, or that they may arise independently of any other; and this is merely extending to insects a generalization very obvious with respect to man—finding warrant for the extension, as we do, in the facts disclosed by an examination of the general economy of insect life.

NOTES AND LITERATURE

BIOMETRICS

Some Recent Studies on Growth.—The problems presented by the phenomena of growth change are not only peculiarly adapted to quantitative treatment, but perhaps more obviously and clearly demand the application of quantitative methods for their solution than does any other single large class of biological problems. In the study of variation and heredity it is an open question as to what relative importance is to be assigned to quantitative as compared with qualitative differences between organisms. But however much interest or significance qualitative changes occurring in connection with the growth process may have, it yet remains an indisputable fact that the fundamental and essential feature of the process is a quantitative change. While this has, of course, always been recognized by students of the subject, there still is to be seen evidence of the influence of the modern biometric standpoint in recent studies in this field. This is chiefly apparent in the increasing attention paid to precision and refinement in the mathematical methods used in the analysis of the distinctively quantitative phases of the problems of growth.

The most recent contribution in the series of memoirs by Professor H. H. Donaldson[1] and his students dealing with various phases of the problem of growth in the white rat is in some respects to be regarded as the most fundamental which has yet appeared. This paper gives in detail the basic data regarding the growth of the body as a whole and of the central nervous system in the white rat which have been collected in the course of a very extensive and thorough investigation. These data are given in a "general table" occupying thirteen pages and comprise records for 458 male and 215 female normal white rats. For each of these animals (with the few omissions of single measurements in scattered individuals unavoidable in so large a piece of work) there are recorded the following data: Series

[1] Donaldson, H. H. A Comparison of the Albino Rat with Man in Respect to the Growth of the Brain and of the Spinal Cord. *Journ. of Comp. Neurol. and Psychol.*, Vol. XVIII, pp. 345–392, Plates II and III, 1908.

number, sex, age in days, body weight, brain weight, and spinal cord weight, each in grams. That the utmost care was taken to ensure the accuracy of these weight records really does not need saying in an American biological journal. The body weights are recorded to a tenth of a gram, and the brain and cord weights to a ten-thousandth of a gram. These unique data, involving thirteen years in the collecting, constitute a scientific achievement of much significance, not alone because of the intrinsic importance of the records for the study of growth problems, but also because they are a monumental example of biological data collected with physico-chemical exactness. The paper will stand as a classic in the literature on growth.

The first portion of the paper deals with the growth of the rat's brain. The brain-weight data are plotted to a base line of body weight instead of to a base line of age and when so arranged are graduated with a curve of the general type.

$$y = A + C \log (x + \beta)$$

where y denotes brain weight, x body weight and A, C and β are constants.

The actual theoretical curve for the brain weight of the white rat is as follows:

$$y = .569 \log (x - 8.7) + .554.$$

This curve gives a very excellent graduation of the observational data. In fact, a closer agreement between theory and observation could not reasonably be expected. It is of some interest to note that this curve which describes the growth of the rat's brain in weight is of the same general type which has been found by Pearson and by the present writer to describe growth changes in various organisms.[2] It is all the time becoming more evident that this type of curve is a very useful one for growth work. Experience is showing that it undoubtedly has a wide range of applicability in describing the quantitative changes occurring in growth and various sorts of regulatory phenomena. While this fact is empirically obvious, no ulterior biological significance is to be attached to it. The biological significance of this fact appears to the present writer to be of the same *kind* as would attach to the discovery that some particular stain was useful for differentiating a wide range of cell

[2] Cf., for example, the data regarding growth in the plant Ceratophyllum presented in Carnegie Institution Publication No. 58.

structures, not before known to have anything in common. Such a result *might* mean that these structures all had a common cause or mode of origin, but to draw such a conclusion in the absence of confirmatory evidence of another kind than that afforded by the stain would be an exceedingly hazardous proceeding.

Donaldson points out that while the logarithmic curve describes very well the growth of the brain for the whole period from birth to maturity, the simpler relation proposed by Dubois, according to which the brain weight increases as some simple proportion (here the seventh root) of the body weight, fails to do this, since it holds only for the later growth period of the rat's brain. It fails entirely to graduate the data during the period of rapid growth.

The second portion of the paper deals with the growth of the spinal cord. This again is found to follow a logarithmic curve of the same general type as that which graduates the brain growth data though, of course, with different values of the several constants. Succeeding portions of the paper deal with the growth of the entire central nervous system and with the comparison of the growth of the brain in the rat and in man. Limitations of space forbid a detailed discussion here of the numerous significant results set forth in the paper. Certain points of particular interest from the biometric standpoint may, however, be touched upon briefly. First with regard to the correlation data, Donaldson finds that the weight of the brain in the white rat is very closely correlated with body weight, the coefficient of correlation between these two variables being $.76 \pm .01$. This appears to indicate a very much closer relationship in this organism than in man, though of course it must always be remembered that the body weight data for man which have been available for the study of this correlation are autopsy records and therefore not too trustworthy. The correlation found between brain weight and age is also very much higher than the corresponding correlation in the case of man, the coefficient here being $.52 \pm .03$. The spinal cord weight is found to be even more closely correlated with body weight than is brain weight; the coefficient being $.86 \pm .01$. Here there are no human data available for comparison. The data presented also indicate a very high degree of correlation between the weight of the brain and the weight of the spinal cord. The coefficient of

correlation here is .88 ± .01. All of these correlation coefficients are positive.

The high values of these correlation coefficients for the rat as compared with man suggest an interesting question: Are we to conclude on the basis of these results (and similar ones obtained by Kellicott from his study of the toad) that there is a general tendency for the various parts of the body to be more closely correlated in lower organisms than in man? In the writer's opinion such a conclusion is at present very doubtful for two reasons. In the first place the human data on which correlation studies have been made are meager and, from their method of collection, not altogether trustworthy. In the second place the coefficients of correlation published by Donaldson (the same considerations hold with reference to Kellicott's toad data, though not to so great a degree relatively) probably have spuriously high values. This arises from the fact that they are deduced from material which is very heterogeneous in respect to age. The biometric constants for all characters which change with age by growth will have their values affected in such material. It is a well-known fact, of which the mathematical proof was first given by Pearson, that heterogeneity of material operates to increase apparent correlation. To such an extent may this occur that several sets of data, each of which taken alone shows no correlation whatever between two characters, may when combined exhibit a high degree of correlation between these characters. Such correlation obviously has little, if any, biological significance. In the work here under discussion no account is taken of the possible effect in increasing apparent correlation of the age (= growth) heterogeneity of the material. It seems desirable if brain-weight (or other) correlations are to have full significance for comparative purposes, that they be based either on adult material in which all growth changes have reached a minimum, or at least on material which is homogeneous in respect to some definitely marked period of the life cycle.

A further point of less practical significance which is apparently overlooked by Donaldson in his discussion of correlation results is that in at least all of his cases in which the regression lines are plotted in the paper the correlation is markedly skew. In such cases, of course, the correlation coefficient can not be taken as the true measure of the actual correlation. Instead, resort must be had to the correlation ratio (η).

The facts regarding the sex relations in the weight of the central nervous system and its growth in the rat are very interesting. Just as in man the brain of the male rat is absolutely somewhat heavier than is that of the female rat of the same body weight. The difference, however, is very small. It is believed by Donaldson that this small difference which remains in favor of the male in respect to brain weight is probably open to further reduction as other variables are taken into account. In general the quantitative relations of the growth of the central nervous system are found to be similar in man and the white rat.

A paper with very much the same general standpoint as the one just discussed has recently been published by Kellicott.[3] The immediate problem with which this paper has to do is stated in the following words (p. 319):

> We are led to inquire whether the normal growth of an animal may not be actually a complex of growth cycles of component parts. It is quite possible to examine this question from the morphological as well as from the physiological side and the present paper represents an attempt to discover whether the brain and viscera of the dogfish grow similarly or in diverse ways as somewhat independent units of growth.

The investigation is based on data obtained from a series of 315 dogfish (176 females, 139 males) including specimens from birth up to those of large size and presumably considerable age (maximum weight observed 8,434 grams). On these fish the weights of the following organs were determined: brain, heart, rectal gland, pancreas, spleen, liver and gonad. In addition the total body weight was determined in each case. The weighings were made in all cases except body weight to hundredths of a gram.

Since it was impossible to determine the exact age of the specimens, the whole of the material is dealt with from the standpoint of total body weight as a base. The author justifies this procedure on two grounds, one necessity, and the other that such factors as "food and temperature are known to be of more importance than age in determining the size of fish."

The specimens studied do not represent a random sample of a fish population, but were especially selected to get a represen-

[3] Kellicott, W. E. The Growth of the Brain and the Viscera in the Smooth Dogfish (*Mustelus canis* Mitchell). *American Journal of Anatomy*, Vol. VIII, pp. 319–353, plates 1–7, 1908.

tative size series. The data so obtained were plotted, each individual being entered separately. Smooth curves were then derived from these and the bulk of the paper is occupied with a discussion of the facts brought out by these smoothed curves. The only statement as to how the observational data were smoothed is the following (pp. 322–323):

> The curves were derived from these records by calculating a series of average weights of each organ in successive groups of individuals and a line formed by connecting these averages was then smoothed to a curve so as to reduce to a minimum the plus and minus deviations of the averages. The groups from which the averages were derived varied in extent from 100 to 1,000 grams in different regions of the entire group, according to the rate at which the character of the curve was changing.

From this the inference would appear to be that the smoothing was done by a free-hand graphical process. If this inference is correct the logical justification of the procedure in the present case is difficult to see. If the curves have enough intrinsic significance to warrant smoothing at all (as these for the dogfish certainly do) it is hard to understand why the smoothing should not be done by an accurate method. Of course cases will arise in practical work where the points to be brought out by data are not of sufficient importance to warrant the labor involved in graduating them accurately. But in the present case the whole discussion centers about the forms and relationships of the smoothed curves.

The point involved here is not a trivial or insignificant one. Any one who has had experience in fitting parabolas and similar curves to observational data knows what unexpected effects on the general contour of a curve a few outlying points may have, when the rigidly "fair" method of least squares is used in the smoothing. The difficulty may be put in this way: in curves of the sort dealt with by Kellicott the observations are very scattering over a considerable part of the total range of the curve. In many instances only two or three observations will be averaged to get a point on the smooth curve. But surely it can not be maintained that the average given by two individuals will uniformly be the same as would appear if 25 individuals were to be used. The two individuals may happen to be the mediocre ones which will give nearly the true average: but on the other hand they are not unlikely (as the right-hand ends of

all of Kellicott's curves except that for brain weight clearly show) to be widely divergent from mediocrity. But the "free-hand" method of smoothing assumes, actually if not intentionally, that the average based on two individuals is just as "right" (*i. e.*, expressive of the true relationship which it is the purpose of the investigation to discover) as is that based on 25. This obvious error any adequate method of curve fitting will avoid.

The bearing of these remarks further appears clearly in the case of some of the relative curves, wherein the percentage which the particular organ weight is of the total body weight is plotted. As was to be expected from what is known of growth in man the general trend of these percentage curves is downward. While this is the general trend, several of the curves (*e. g.*, the heart curve, plate 2) show at the very beginning a slight rise to a maximum and then the downward curve. It is plain from the discussion that Kellicott considers the rise at the beginning of these percentage curves to be a real and significant phenomenon of growth. It is very doubtful, however, whether the data warrant such a conclusion. Before accepting it one would like to see the measurements of a much larger number of very young (*i. e.*, just hatched) individuals added to the curves, and then have a curve fitted by some adequate method to the observations.

The general result of this interesting and careful piece of work is to show that the regression line of organ weight on body weight in dogfish of different sizes is not of the some form for all organs. Some organs (*e. g.*, rectal gland, pancreas) show a nearly linear increase in weight as the body increases in size; others (*e. g.*, the brain) show the logarithmic like curve which one associates with growth curves. The author gives an interesting discussion of the significance of the fact that the muscular and skeletal tissues tend to "outgrow" their visceral accompaniments in forms of indeterminate growth like the dogfish. He regards the condition of determinate growth seen in higher vertebrates as "an adaptation on the part of the organism, such that muscles and supporting tissues cease their growth at such a point that brain and viscera remain competent to maintain a physiological balance."

In passing it may be noted that Kellicott's work, while itself strictly morphological, suggests on every page problems for experimental work on the physiology of the growth process. In

this connection a recent paper by Burnett[4] is of interest. This paper, though not specifically concerned with growth problems as such, brings out in a very clear way the marked differential effect which may be produced on a single organ system (the skeleton) by differences in the food of the growing animal. Different foods, with all other conditions constant, led to an average difference in the breaking strength for five bones of the body of 356 pounds per 100 pounds body weight. The relative magnitude of this difference is indicated by the fact that the *maximum* observed average breaking strength was 681 pounds per 100 pounds of body weight. This difference is brought about not by an increase in the size of the bone as a whole, but by a thickening of its walls. Burnett's detailed results are well worth careful study from the standpoint of experimental morphology.

A new and suggestive view in regard to the ultimate physiology of the growth process has been put forth recently in two papers by Robertson.[5] In brief this view is stated by the author in the following words (first paper, p. 612):

1. In any particular cycle of growth of an organism or of a particular tissue or organ of an organism the maximum increase in volume or in weight in a unit of time occurs when the total growth due to the cycle is half completed.

2. Any particular cycle of growth obeys the formula $\log x/(A-x) = K(t-t_1)$ where x is the amount (in weight or volume) of growth which has been attained at time t, A is the total amount of growth attained during the cycle, K is a constant and t_1 is the time at which growth is half completed.

3. The above relations are such as would be expected to hold good were growth the expression of an autocatalytic chemical reaction. As I have pointed out in the introduction, cell-division has been shown by Loeb to be the expression of an autocatalytic synthesis of nuclear material. The fact that the above relations hold good shows that, in all probability, cell-growth, or the synthesis of cytoplasm, is also an autocatalytic reaction.

These conclusions, if well founded, are certainly of very fundamental importance. It therefore seems desirable to ex-

[4] Burnett, E. A. The Effect of Food on the Breaking Strength of Bones. Bulletin 107, Nebr. Expt. Stat., pp. 11–39, 1908.

[5] Robertson, T. B. On the Normal Rate of Growth of an Individual and its Biochemical Significance. *Arch. f. Entwicklungsmech.*, Bd. 25, pp. 581–614, 1908. Further Remarks on the Normal Rate of Growth of an Individual and its Biochemical Significance. *Ibid.*, Bd. 26, pp. 108–118, 1908.

amine with some care the nature of the reasoning and the evidence on which the conclusions rest. The first point in this regard to be noted is the fundamental assumption made by the theory that the growth process is in its quantitative relations *determinate* either as a whole, or in its cyclical units. In the fundamental formula quoted A is the total amount of growth attained in the cycle. This means that unless there is assumed to be an indefinitely large number of cycles of growth, there comes a time for every organism to which the theory is to be applied, after which no more growth occurs. Regarding this fundamental assumption of Robertson's theory Kellicott, whose own researches particularly well fit him to speak with authority on the point, has the following to say (*loc. cit.*, p. 342):

> Observations of many of the lower vertebrates in nature (Fulton, '01, '06) and in captivity, such as the giant salamander and some reptiles, show that these grow indeterminately; Agassiz's, '57, observations upon Chrysemys are typical. As a recent example of the failure to make this distinction we might mention the work of Robertson, '08, who has devised certain formulæ for the description of growth and has brought out the very suggestive fact that the growth curve of an organism or organ or tissue is similar to that given by an autocatalytic reaction. These formulæ hold good upon the assumption that the organism or organ has a definite period of growth at the end of which increase in size ceases. This is true for the higher vertebrates, but for all the indeterminately growing forms we can not determine any such "final weight" of the body or organ upon which to base a formula. We could not assume the maximum discovered size as the "final weight" because this is subject to such extreme variation; in the dogfish, including both sexes, we might find the "final weight" anywhere from 2,000 to 8,000 grams and even higher.

That this point has some force in limiting the field of application of Robertson's view can not be denied. It would still appear to be possible to apply the theory to lower vertebrates and invertebrates, however, on the assumption that growth in those cases consists of an indefinite number of cycles, to each one of which separately the "law" applies. It remains to be investigated as to whether the growth in such forms is, as a matter of fact, definitely cyclical in character.

The general line of reasoning adopted by Robertson in developing his theory of growth is as follows: The starting point is the idea advanced by Loeb "that the process of synthesis of nuclein, which is the most salient phenomenon immediately suc-

ceeding fertilization, partakes of the characteristics of an autocatalyzed chemical reaction, since the velocity of the synthesis increases, during the initial stages of cell-division, in proportion as nuclear material has already been synthesized." He then raises the question as to whether the formation of fresh cytoplasm during the growth of an organism may not also be an autocatalytic reaction. It is pointed out that:

> The increase in weight or volume of an organism may not improbably be regarded as equivalent to an increase of cytoplasm, and if both of the processes concerned in growth, namely nuclear and cytoplasmic synthesis, are autocatalytic in character the increase in weight or volume of an individual with increase of time should display the quantitative relations which are characteristic of an autocatalytic chemical reaction. In the first place the temperature coefficient of growth should be that of a chemical reaction; in the second place the relation between body weight or body volume and the time which has elapsed since measurable growth began should be the same relation as that which subsists between the mass of material which has undergone a chemical change and the time in an autocatalytic reaction.

This work of Peter is cited to show that the temperature-coefficient of cell division and of growth is that of a chemical reaction. Robertson's own papers are solely concerned with the presentation of evidence to show that growth curves of organisms are of the same type as the curve of an autocatalytic reaction.

Various observations on the growth of certain animals, plants and man are cited from the literature. To each group of these data the theoretical curve of an autocatalytic reaction is fitted. Theoretical and observational curves are then compared, and it is maintained that the graduations obtained are good ones. The agreement between observation and theory which is held to be shown by these comparisons is the only new evidence presented by Robertson in support of the conclusions quoted above.

The data presented in the papers may first be considered with reference to the soundness of the contention on which the whole reasoning ultimately rests: namely, that the theoretical curve for an autocatalytic reaction actually does give a good fit for observed growth data. A careful, critical study of the data presented in the two papers indicates that in general the correspondence between theory and observation is very far from being sufficiently close to warrant the conclusion that such is the case. To bring this point out in a concrete fashion let us

examine some of the tables given. Table I of the first paper (pp. 581–591) deals with Donaldson's[6] data on the growth of the male white rat in respect to body weight. In this table are given the observed body weights for rats of different ages and the calculated body weights according to the autocatalytic growth curve. In addition there is given a column showing the differences in grams between the observed and the calculated body weights. Now it is a first principle of scientific curve fitting (and on this point science and common sense are as usual in agreement) that a curve which gives a good graduation of observational data will fairly and equably distribute the errors. That is to say, a theoretical curve if it is to be regarded as fitting the data should strike through the observations in such way that there will be on the average as many and as great differences where theory is in excess of observation as there are where it is in defect of observation. If a great majority of the differences between theory and observation are in one direction there is clearly a bias and the theoretical curve can not fairly be said to be an adequate representation of the observations. Now, let us examine the actual facts for Robertson's Table I. In this table are included 63 separate observations or ordinates. In one case out of the 63 the theoretical and the observed ordinate exactly agree. Of the remaining 62 cases where theory and observation can be compared the calculated ordinate is greater than the observed in only 14. The observed ordinate is greater than the calculated in 48 cases out of the 62. Furthermore, the total deviation between observation and theory when theory is greater than observation is 19.6, whereas when observation is greater than theory the total deviation is 706.0! This certainly does not look like a fair distribution of the errors when in 77 per cent. of the ordinates the theoretical curve lies always on the same side of the observational line.

Let us turn to Table II. This table is exactly like Table I except that it deals with Donaldson's data for the growth of female white rats in body weight, whereas Table I deals with the males. In this table there are in all 50 ordinates. Of these one again shows an exact agreement between observation and theory. In 43 or 88 per cent. of the remaining 49 ordinates the calculated value is less than the observed. Only in 6 cases is the calculated value greater than the observed! Practically the

[6] Boas Memorial Volume, New York, 1906.

whole of the theoretical curve in this case lies on the same side of the observed line. The sum total of the plus deviations equals only 1.15, whereas the sum total of the minus deviations equals 199.05!

Let us take still another example, this time from near the end of the first paper. In Table IX (p. 610) are presented Donaldson's[1] data regarding the growth of the brain in the frog and the fitted curve. In this table are 21 ordinates available for the comparison of theoretical curve and observational data. The deviation between theory and observation is plus in 18 out of the 21 cases and minus in 3 cases only. Two ordinates (making with the 21 the total of 23 tabled) show exact agreement between theory and observation. In spite of this extraordinarily uneven and biased distribution of the errors this statement follows Table IX:

It is evident that the agreement between theory and observation is excellent, such divergences as exist being evidently irregular and accidental in their nature.

Surely a system of errors in which 86 per cent. are in excess and only 14 per cent. are in defect and in which the *mean* percentage deviation per ordinate for the plus deviation is 8 per cent. can not fairly be said to be "irregular and accidental" in its nature.

Other examples showing the same thing might be cited from the papers. The tables which have been chosen as illustrations of the point under discussion have been taken in preference to others for two reasons: one that they were long tables, involving a fairly large number of ordinates, the other that the observational data in these tables were obtained by most careful and painstaking measuring and are absolutely trustworthy. On such data, if anywhere, a theoretical curve may fairly be expected to give good results.

To summarize this part of the discussion it may be said that the discrepancies between observation and theory are so great in amount, so biased in character and so frequent in the data presented that these data, as they stand, can not reasonably be held to afford evidence of any particular value in favor of Robertson's ingenious, suggestive and potentially very valuable hypothesis. It is possible that better values for the constants of the theoretical curves might be found and in this way better

[1] *Jour. Comp. Neurol.*, Vol. VIII, 1898.

agreement between theory and observation be obtained. Until this is tried it would appear to be impossible to form any just and significant estimation, on the basis of the only *kind* of evidence which Robertson presents, namely, the comparison of curves, as to the value of his theory as a general theory of growth. On many general grounds the theory is particularly suggestive. Can not evidence of another and more convincing kind than that adduced in the present papers be brought forward in its support?

The kind of evidence under discussion, when used for a purpose like the present one, can at best have but inferential significance; it can never be of demonstrative worth. It is based on a process of reasoning which assumes a fundamental or necessary relationship to exist between two sets of phenomena because the same curve describes the quantitative relations of both sets. A little consideration indicates that this method of reasoning certainly can not be of general application, even though we assume it to be correct in particular cases. The difficulty arises from the fact that the mathematical functions commonly used with adequate results in physical, chemical, biological and mathematical investigations are comparatively few in number. The literature of science shows nothing clearer than that the same type of curve frequently serves to describe with complete accuracy the quantitative relations of widely different natural phenomena. As a consequence any proposition to conclude that two sets of phenomena are causally or in any other way fundamentally related solely because they are described by the same type of curve is of very doubtful validity. A few examples will make clear the point here under discussion.

In a recent paper Armsby[8] shows that the rate of gain of protein per thousand pounds live weight in growing animals follows extremely closely the following curve: $g = 135/(a + 20)$, where g is gain in protein per day per 1,000 lbs. live weight and a is age in days. This curve, as his Fig. 1 clearly shows, fits the observational data at hand remarkably well. This equation is the equation of a rectangular hyperbola. But it is a well-known fact that the relation between degree of dissociation and degree of dilution in dilute solutions is given by a hyperbola. Now in so far there would appear to be exactly the same

[8] Armsby, H. P. Feeding for Meat Production. Bureau of Animal Industry, Bulletin 108, pp. 1–89, 1908.

kind of logical basis for the conclusion that since the same curve describes the rate of protein gain in growing animals as describes dissociation phenomena, therefore rate of protein gain is a dissociation phenomenon, as would exist for the conclusion that growth is an autocatalytic reaction provided there were good agreement between observed and theoretical curves in the latter case. A point of difference in the two cases is that Robertson presents several curves in support of his conclusion, whereas Armsby gives but a single hyperbola. But even this difference is in some degree offset by the fact that Armsby's curve involves growth data from four different animals collected by a number of observers. But the most ardent advocate of the plan of deducing fundamental relationships from similarity of curve type would not maintain that the rate of protein gain in growing animals is in any causal or fundamental way directly related to the phenomenon of dissociation in dilute solutions.

Let us take still another case. One of the fundamental gas laws is that the "pressure of any given mass of gas varies directly as the absolute temperature if the volume of the gas remains constant." The mathematical expression of this relation is the equation of a straight line. Now Galton, Pearson and their co-workers have shown, with a wealth of data drawn from man and other organisms, that the regression of offspring on parent in parental inheritance is a linear function. If the mean conditions of a characteristic of the offspring of each group of parents be plotted these plotted points will fall on a straight line, within the errors of random sampling. This result rests on a great mass of exact measurements. But of course no one would attempt seriously to maintain that parental inheritance and regression are phenomena of gas pressure.

The point which the writer would make is this: If there is good evidence *on other than quantitative grounds* that two sets of phenomena are qualitatively alike it is is pertinent and significant to present as additional and confirmatory evidence data tending to show that these sets of phenomena are similar in their quantitative relations. But similarity of quantitative relations between phenomena can not safely be taken as proof (or, in the absence of qualitative data sufficient alone practically to establish the point, even as particularly weighty evidence) of qualitative identity, because of the observed general lack of uniqueness in the quantitative relations of natural phenomena.

In a word the final *proof* of qualitative identity of phenomena must always in last analysis be qualitative in its nature; quantitative evidence in such cases can at best have but an inferential confirmatory bearing on the qualitative point at issue.[9]

RAYMOND PEARL.

EXPERIMENTAL ZOOLOGY

Are the Drone Eggs of the Honey-Bee Fertilized? Cuénot[1] has put to the test once more Dzierzon's famous theory in regard to the nature of the drones of the hive bee. Dzierzon, as is well known, furnished strong evidence in favor of the view that the egg that produces a drone is not fertilized. An obvious test of this view is found in crossing a virgin queen of one race by a male of another race. All of her worker offspring should be hybrids but her drone offspring should be purely maternal in character. It is said that the failure of one such experiment to give the expected results caused Dzerzon to abandon temporarily his theory. Other workers too have from time to time found that the drones in such cases sometimes show hybrid characters and this argument has been repeatedly urged against Dzierzon's theory despite the large amount of evidence of a different kind to the contrary.

Cuénot crossed a virgin female of the black or Italian bee of pure race with a "yellow bee" also of pure race. All the workers produced showed the yellow bands of the yellow parent; some 300 drones were black like the mother, two only showed a large yellow band at the top of the abdomen (recalling the more numerous yellow bands of the yellow bee), and about a dozen other males also showed some yellow bands on the abdomen. "Do those yellow bands indicate hybridization?" Such bands were never found in the males of neighboring hives. The experiment is inconclusive, Cuénot says, but it shows the necessity of examining not only the purity of the pure races but also the extent of their variation. The possibility that these few hybrid males may have arisen from eggs laid by the hybrid workers is not considered by Cuénot but until this possibility is also excluded the results can not be maintained to show the hybrid nature of the drones except in the latter sense. If the males

[9] Cf. the discussion regarding the simple logarithmic growth curve on p. 304, *supra*.

[1] Cuénot, L. *Comp. Rend. Soc. Biol.*, LXVI, 1909.

have arisen as here suggested from the eggs laid by the hybrid workers the fewness of such individuals in comparison with the large number of pure males is explained. On the other hand the apparently well established view that drones come from unfertilized eggs does not exclude the possibility that fertilized eggs might also under certain exceptional conditions produce males.

T. H. MORGAN.

THE UPHOLDING OF DARWIN

Poulton and Plate on Evolution.—The boundary lines of political geography are supposed to have no influence in determining scientific beliefs. In science one is cosmopolite. But hedged in by a nation's boundaries is a people of one blood, men of a common genealogy, and hence of some identity of hereditary endowment. It may not be so easy, therefore, for an Englishman to be French in scientific tenets as he may imagine. The coincidence that the majority of conspicuous English biologists, such men as Wallace, Galton, Lankester, Archdall Reid, Edward Poulton and others, hold so strongly to the natural selection dogma, and, except for the German founder of the school, are the most outspoken upholders of neo-Darwinism, may be indeed more than a coincidence. It may be unconscious scientific patriotism. And so in France, there is no question of the strong leaning of present-day French biology toward Lamarckism. How much more pitiful, in the light of this fact, let us add, seem the neglect and contempt of the great French evolutionist in his lifetime by his Gallic colleagues! But he has now his reward. Scientific patriotism is bringing his name and his teaching to be the glory of French biology.

I would not press my theory too hard. As Weismann is the founder of neo-Darwinism the Germans ought to be neo-Darwinists, but they mostly are not: and as Haeckel is a monist, they ought mostly to be anti-dualists, but again they mostly are not. Also, as America is more Anglo-Saxon than Latin, we ought to be more Darwinian than Lamarckian, but we are not. So my theory, like many another of even greater plausibility, but ill stands hard wear. Even in England there are men who see other factors in evolution than natural selection, and to tell the truth these men in the minority are after all the truer upholders of scientific patriotism, for like them Darwin also saw

other agents than selection that made for modification and descent. And so my theory, perhaps, wears quite through and should go to the rag-bag.

The latest conspicuous exposition of the English neo-Darwinian point of view is that embodied in Professor Poulton's "Essays on Evolution" (1908, Oxford). Not that the essays themselves are "latest," for their various dates cover the decade between 1896 and 1906, but they are put out now, with revisions and some additions, as the expression of the distinguished author's present point of view. This is clearly and strongly that of a neo-Darwinian, a thoroughgoing selectionist.

The most important and interesting parts of the book are certainly those in which the author exposes the facts and theories of insect mimicry and uses them for argument. These facts and theories are not only the field in which Professor Poulton is especially at home—a field, indeed, which he practically owns —but are also the field in which lie some of the most potent testimony for the deification of selection. Weismann and other neo-Darwinians have never overlooked the stumbling block to Lamarckians and orthogenesists that protective resemblance, warning colors and mimicry constitute, but Professor Poulton with his immense resources of personal knowledge in this field makes to the same end, far more effective use of the facts. The least pleasing and, for that matter, least profitable part of the book to its readers is the polemic introduction, far too bitter and personal, discussing "mutation, Mendelism and natural selection." It mars the book.

The essays cover a wide range of subjects: "The age of the earth"; "the definition of species"; "Huxley and selection," in which is maintained the surprising thesis that the great champion of Darwin "was at no time a convinced believer in the theory he protected"; "a remarkable anticipation of modern views on evolution," in which Weismann's arguments against the inheritance of acquired characters are shown to have been in rather full measure advanced by James Cowles Prichard, the English anthropologist, in 1826; "theories of heredity." "theories of evolution," and, most extensively and importantly, the facts and theories of insect mimicry. The exposition of these in the last three chapters and special index, is not only most fascinating and stimulating reading but it will serve until we can have the author's promised more extended treatment

in a future book as the latest authoritative exposition of the subject. The book is completed by an amazing analytical index of eighty-three pages, one sixth of the whole book. No reviewer will ever be able to taunt Professor Poulton with that too familiar, "we regret to note the insufficiency of the index."

Finally an entomologist may be pardoned for "pointing with pride," in connection with this book to the splendid work for evolution and general biology that the insects have achieved, in the tireless and skillful hands of Professor Poulton. They have painted a wonderful picture in colors of the possibilities of adaptation and the marvelous capacity of selection—or some other factor. For the moment selection has all the best of the presumption, but this may depend in considerable measure on its great good fortune in the strength of its champion. There is certainly no gainsaying this strength. Professor Poluton, entrenched in his special field of insect bionomics, is perhaps the most serious antagonist that the neo-Lamarckians have to face.

Of somewhat different point of view, and wholly different type, is the other book of Darwinian upholding, which I have at the moment under my eyes. In 1899 Ludwig Plate of the Berlin Landwirthschaftliche Hochschule delivered an address at the meeting of the Deutsche Zoologische Gesellschaft in Hamburg, which was printed in the proceedings of the society under the title "*Über die Bedeutung des Darwin'schen Selections-prinzips.*" This address both as spoken and printed attracted much attention and the demand for it induced Professor Plate to expand and reprint it in book form in 1903. The admirable comprehensiveness of the discussion in the new form still further increased the interest and demand, as a result of which we have now a revised and still more expanded third edition of nearly 500 pages (twice the size of the second edition) under the title: "Selectionsprinzip und Probleme der Artbildung," with the subtitle "Ein Handbuch des Darwinismus" (1908, Engelmann, Leipzig). The author in the meantime has been made a professor of zoology in the University of Berlin as well as in the Landwirthschaftliche Hochschule.

Plate is an able friend and defender of selection, but his point of view is not that of Poulton. The Englishman holds rigidly to the neo-Darwinian anti-Lamarckism; the German takes the real standpoint of Darwin, he calls on the inheritance of acquired characters to aid selection in its evolutionary task. He

fights Weismanism in almost all of its aspects: panmixia, germinal selection, *Allmacht* of selection. He resists also any serious encroaching of the mutation theory in the province of species-forming and adaptation. His detailed account and reasoned criticism of De Vries's famous theory are admirable. Isolation, especially those forms of it which may be classified under the general head of "Biologic isolation," is treated *in extenso*. In this connection Plate opposes those statements of Wagner and D. S. Jordan, which claim that new species do not arise, or do so only very rarely, in the same geographic range. He refers to the hundred *Gammarus* species in Lake Baikal, the numerous Cladoceran species of *Bythotrephes* in the Caspian Sea, and the eighty or more chromid kinds in Lake Tanganyika, as examples of nearly related forms that have long inhabited the same limited region and yet among which evolution has steadily gone forward. He discusses the old question of the inheritance of acquired characters in a new way, and those pages in which he explains and justifies his admission of the logical necessity of such an inheritance to explain certain types of adaptation constitute one of the most important parts of the book. His treatment of the Darwinian theory of sexual selection and candid admission of its weaknesses is another admirable instance of the broad-mindedness of this Darwinian champion. Finally his account of the objections to selection and their refutation or recognition as partly valid is simply complete, as is his consideration of the species-forming theories auxiliary to selection.

But this fugue of praise grows monotonous, and yet it is hard to introduce any new measure. Perhaps the sparse scattering of pictures may be criticized as being far too meager if illustration was really needed, and easy reading of the text is a little interfered with by the introduction of date and page references into the lines; but these are trifles. The book is excellent arranged both for logical sequence of presentation and for easy reference to any particular phase or topic of the wide subject treated. Professor Plate's acquaintanceship with the active work now going on along the various lines of evolution study and with the literature of the whole subject is manifestly nearly exhaustive. It is especially pleasant to note his generous recognition of American work.

V. L. K.

PARIS, March, 1909.

The American Journal of Science

Established by Benjamin Silliman in 1818.

The Leading Scientific Journal in the United States

Devoted to the Physical and Natural Sciences, with special reference to Physics, and Chemistry on the one hand, and to Geology and Mineralogy on the other.

Editor: EDWARD S. DANA.

Associate Editors: Professor GEORGE L. GOODALE, JOHN TROWBRIDGE, W. G. FARLOW and WM. M. DAVIS of Cambridge; Professors A. E. VERRILL, HENRY S. WILLIAMS and L. V. PIRSSON, of New Haven; Professor G. F. BARKER, of Philadelphia; Professor JOSEPH S. AMES, of Baltimore; MR. J. S. DILLER, of Washington.

Two volumes annually, in monthly numbers of about 80 pages each.

This Journal ended its first series of 50 volumes as a quarterly in 1845; its second series of 50 volumes as a two-monthly in 1870; its third series as a monthly ended December, 1895. A Fourth Series commenced in 1896.

Subscription price, $6 per year or 50 cents a number, postage prepaid in the United States; $6.25 to Canada; $6.40 to countries in the Postal Union. Back numbers at reduced prices.

☞Ten-volume Indexes, Vols. I-X, XI-XX, fourth series, price one dollar. Address

The American Journal of Science
New Haven, Conn.

Pour paraître en 1908.

LAMARCK

sa vie, son œuvre
par MARCEL LANDRIEU.

1 vol. gr. in 8° raisin d'environ 550 p. avec un portrait en hèliogravure et renfermant de nombreux documente inédite.

Sera publié dans les Mémoires de la Société Zoologique de France et mis en vente également au prix de **10 fr.** Le tirage étant trés limité, prière de souscrire immédiatement en s'adressant au Secrétaire général,

28 RUE SERPENTE, PARIS.

To Zoologists and Museums
W. F. H Rosenberg
Importer of Exotic Zoological Specimens

57 Haverstock Hill London, N. W. England

Holds the largest stock in the world of specimens in all branches of Zoology.

Just published, my new price list of BIRD'S EGGS, containing over 800 species from all parts of the world. Also price lists Nos. 6, Bird Skins (over 4,300 species), and 7, Mammal Skins, Skeletons, and Spirit Specimens (over 300 species).

Any of the above price lists sent post-free on application.

Science

A weekly journal, established in 1883, devoted to the advancement of the natural and exact sciences, the official organ of the American Association for the Advancement of Science, publishing original articles and notes on the progress of the different branches of science, the proceedings of scientific societies and academies, reviews of scientific books and articles, preliminary accounts of researches and full discussion and news on all subjects concerning scientific men and scientific and educational institutions.

Annual subscription $5.00. Single numbers 15 cents.

The Popular Science Monthly

An illustrated magazine, established in 1872, devoted to the diffusion of science, publishing articles by leading authorities in all departments of pure and applied science, including the applications of science to education and society.

Annual subscription $5.00. Single copies, 50 cents.

The American Naturalist

A monthly journal, established in 1867, devoted to the biological sciences with special reference to the factors of organic evolution.

Annual subscription $4.00. Single numbers, 35 cents.

**** To new subscribers mentioning this advertisement and enclosing one dollar, SCIENCE will be sent for three months, or THE AMERICAN NATURALIST for four months or*

THE SCIENCE PRESS

Garrison, N. Y. Lancaster, Pa.

Sub-Station 84, New York.

EDUCATION WITH REFERENCE TO SEX

Eighth Yearbook of the National Society for the Scientific Study of Education

By CHARLES RICHMOND HENDERSON

THIS study, which was made at the request of the Executive Committee of the Society, and published after their critical examination, and upon the approval of three medical advisors who have read it, is divided into two parts. The first part is chiefly medical and economic, and seeks to prove the necessity for social control of some kind. Medical authorities are cited to show the nature and prevalence of venereal diseases, and of the physical, economic, and moral loss due to the abuses of sexual life. The various methods of police and administrative control in Europe and America are described and critically discussed. The fundamental cause of the evil is found to lie too deep in nature, habit, ignorance, and social neglect to be reached by merely external police measures.

This argument demonstrates the necessity for education with reference to sex—the theme of the second part of the work. In this part is found a careful discussion of educational aims, the scope of educational activities, the co-operating agencies in education, the care of infancy, personal hygiene and training, the influence of ideal interests, the principles of formal instruction in relation to sex—its necessity, difficulties, and methods. The distinctive needs of childhood, adolescence, and maturity are treated with care, and the possible modes of instruction in the schools of various grades are presented. The duties of normal schools, of the religious organizations, and of parents, in view of the situation, are set in the light of the facts. In the appendix is printed a valuable paper by Dr. Helen Putnam, president of the American Academy of Medicine, and also translations of important recent discussions of German teachers.

The author is president of the Chicago Society of Social Hygiene, and associate member of the American Academy of Medicine, and a Professor of Sociology in the University of Chicago.

Part I, 75 pages, 8vo, paper; net 75 cents, postpaid 78 cents.
Part II, 100 pages; net 75 cents, postpaid 80 cents.

ADDRESS DEPT. 62

THE UNIVERSITY OF CHICAGO PRESS

CHICAGO NEW YORK

VOL. XLIII, NO. 510 JUNE, 1909

THE AMERICAN NATURALIST

A MONTHLY JOURNAL
Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

CONTENTS

Page

I. Heredity and Variation in the Simplest Organisms. Professor H. S. JENNINGS 321

II. The Color Sense of the Honey Bee—Is Conspicuousness an Advantage to Flowers? JOHN H. LOVELL 338

III. Variation in the Number of Seeds per Pod in the Broom, Cytisus scoparius. Dr. J. ARTHUR HARRIS 350

IV. Present Problems in Plant Ecology:
The Trend of Ecological Philosophy. Professor HENRY C. COWLES . . 356
The Present Problems of Physiological Plant Ecology. Dr. BURTON LIVINGSTON 369

V. Notes and Literature: Notes on Evolution, V. L. K. DeVries's Species and Varieties, DR. GEORGE H. SHULL. *Embryology*—On the Totipotence of the First Two Blastomeres of the Frog's Egg, DR. J. F. MCCLENDON . . . 379

THE SCIENCE PRESS

LANCASTER, PA. GARRISON, N. Y.

NEW YORK: SUB-STATION 84

The American Naturalist

MSS. intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS

Lancaster, Pa. Garrison, N. Y.

NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

Important New Scientific Books

PUBLISHED BY THE MACMILLAN COMPANY

Botany

The Origin of a Land Flora. A Theory based upon the facts of Alternation. By F. O. BOWER, Sc.D., F.R.S. With numerous illustrations.

Cloth, gilt top, xi+727 pp., illus., index, 8vo, $5.50 net.

NOTE.—A profound study in the morphology of the lowest forms of plants, with special reference to the development of their reproductive systems. The author endeavors to show that the present land flora has originated from an aquatic ancestor, and traces the methods of specialization to the land habit, and the establishment of the forms of the higher plants. A book of the highest importance not only to botanists but to biologists in general.

NEW AND STANDARD HAND-BOOKS ON AGRICULTURE, ETC.

Elements of Agriculture, Southern and Western. By W. C. WELBORN, B.S., M.S., M.P.A.

Cloth, xvi+329 pp., illus., appendix, glossary, index, 12mo, $.75 net.

NOTE.—This is a thoroughly modern treatise on farming as practiced in the Gulf States, rrom the point of view of the scientific agriculturist. It is adapted to school use, but is of practical service to any farmer in that part of the country. The author is vice-director of the Texas Experiment Station.

Re-issues of the highly valued Hand-Books known as the Garden Craft and Rural Science Series, edited by L. H. BAILEY, of Cornell University, Editor of "Cyclopedia of American Horticulture," "Cyclopedia of American Agriculture," etc.

The Principles of Fruit Growing. By L. H. BAILEY.
Tenth Edition, $1.50 net, by mail $1.66.

Irrigation and Drainage. By F. H. KING.
Fifth Edition, $1.50 net, by mail $1.68.

Principles of Vegetable Gardening. By L. H. BAILEY.
Sixth Edition, $1.50 net, by mail $1.68.

Bush Fruits. By FRED W. CARD.
Fourth Edition, $1.50 net, by mail $1.66.

Fertilizers. By EDWARD B. VOORHEES.
Tenth Edition, $1.25 net, by mail $1.38

Farm Poultry. By GEO. C. WATSON.
Sixth Edition, $1.25 net, by mail $1.42

Published By **The Macmillan Company** 64-66 5th Ave., New York

THE

AMERICAN NATURALIST

VOL. XLIII | *June, 1909* | No. 510

HEREDITY AND VARIATION IN THE SIMPLEST ORGANISMS [1]

PROFESSOR H. S. JENNINGS

JOHNS HOPKINS UNIVERSITY

UNICELLULAR animals present all the problems of heredity and variation in miniature. The struggle for existence in a fauna of untold thousands showing as much variety of form and function as any higher group, works itself out, with ultimate survival of the fittest, in a few days under our eyes, in a finger bowl. For studying heredity and variation we get a generation a day, and we may keep unlimited numbers of pedigreed stock in a watch glass that can be placed under the microscope.

Work in this field, so far as it has yet been carried, gives in simple form results which are typical of the trend of investigation over the entire subject; it gives a sort of diagram of the main facts of heredity and variation. For this reason it appears worth while to present here the main results in their bearing on general questions. Technical accounts of the investigations have been published elsewhere,[2] but these are rather forbidding, owing

[1] A paper read before the Scientific Association of Johns Hopkins University.

[2] Jennings, H. S., "Heredity, Variation and Evolution in Protozoa." I, "The Fate of New Structural Characters in Paramecium, with Special Reference to the Question of the Inheritance of Acquired Characters in Protozoa," *Journ. Exper. Zool.*, 5, 1908, 577–632. II, "Heredity of Size and Form in Paramecium, with Studies of Growth, Environmental Action and Selection," *Proc. Amer. Philosophical Soc.*, 47, 1909, 393–546.

to the mass of statistical data involved. For the evidence of the statements here made the reader is referred to these.

Unicellular organisms are essentially free germ cells —germ cells that are subjected to the immediate action of the environment, both direct and selective. For long periods they propagate without that intercrossing which so tremendously complicates the study of heredity in higher animals. Here if anywhere we should see readily the effects of environment and of selection in modifying a race.

Let us look first at the direct action of the environment: the "inheritance of acquired characters." It has commonly been thought that under the conditions found in these organisms "acquired characters" are readily inherited. This is because the progeny arise by division of the parents; they are therefore the *same* as the parent. It would seem a matter of course therefore that they should have the same characteristics as the parent, however these characteristics arose.

But when we examine just what occurs in the production of the new individuals, we find—as usually happens when we look closely at biological processes—that the thing is not so simple after all. We find that in reproduction the characteristic features of the parent disappear[3] and are produced anew in the offspring. Thus in Paramecium (Fig. 1) the characteristic form of the ends, the oral groove, the shape of the body—these disappear during fission, and reappear in the growth of the young. In Stylonychia (Fig. 2) all the appendages are absorbed at division; they appear anew in the young, in their characteristic structure, number and distribution, by a process comparable to the development of organs in a higher animal.

[3] Certain exceptions to this, of no theoretical importance, are mentioned in the original papers. Certain characters sometimes pass directly to *one* of the offspring, but their multiplication is of course always by new production.

Reproduction in these creatures may then be compared to the dissolving of a crystal in its mother fluid; on re-crystallization the new crystal appears with the same form and angles as the parent. But it is really a new

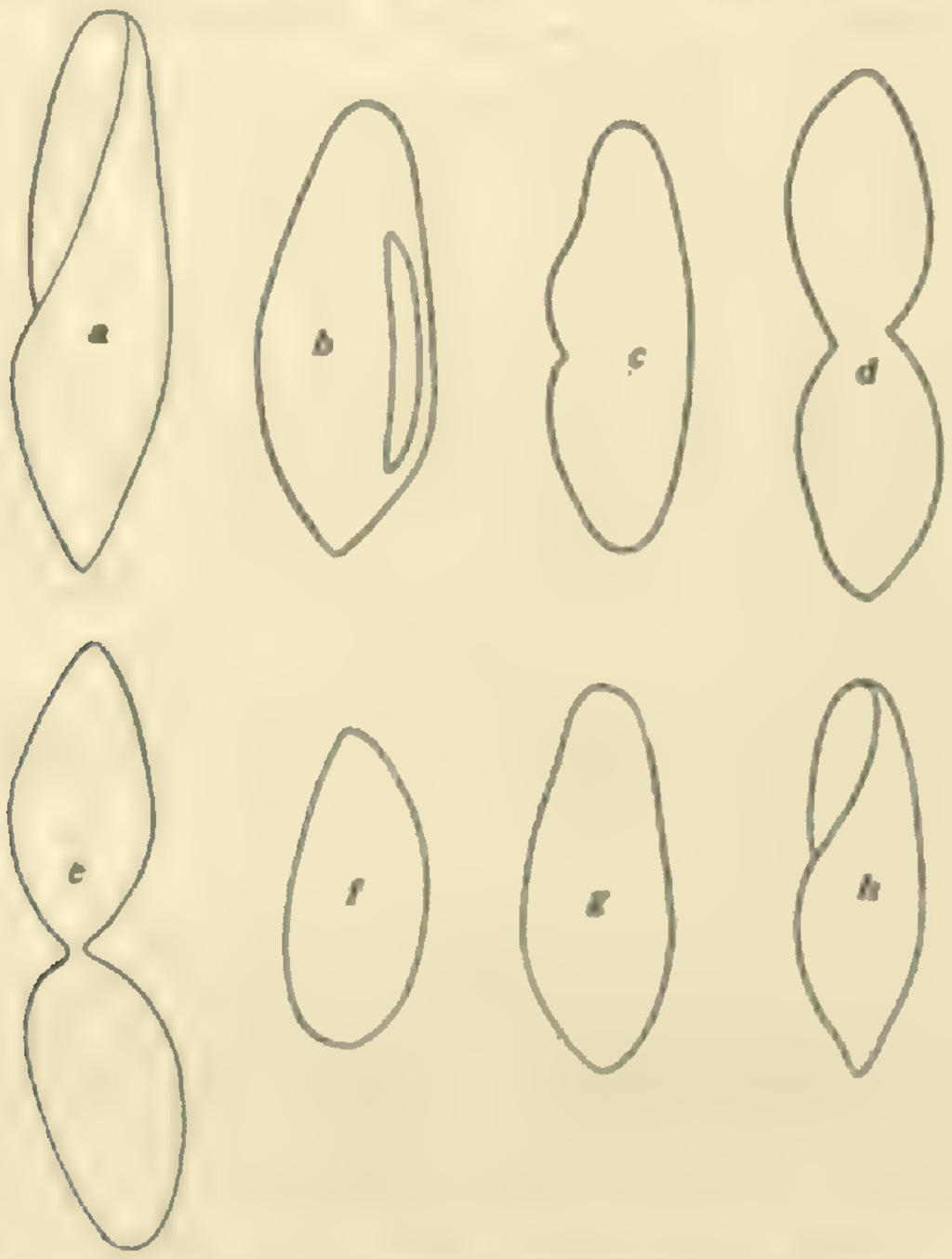


FIG. 1. Changes in form shown by Paramecium during reproduction. *a*, form of adult; *b* to *e*, successive stages of fission; *f*, *g*, immature young; *h*, young after reaching adult form.

FIG. 2. Stylonychia, after Wallengren. *a*, adult, showing the appendages; *b*, stage preparatory to fission. At *x* and *y* have appeared the beginnings of the new sets of appendages of the two progeny to result from fission, after the disappearance of the old appendages.

crystal, with new-formed angles. The analogy of reproduction with recrystallization is striking in many ways, as we shall see farther.

Thus inheritance is, here as elsewhere, not transmission but new production. The question of heredity then is: What characters will thus be produced anew? Will the progeny reproduce *any* character that the parent happens to have?

When we study the matter in such an organism as Paramecium (Fig. 1), we find that all the characters common to the race—the "normal" characters—are regularly reproduced. But how about characters that are not typical; characters that have been produced in the individual parent by the environment; "abnormal" characters, and the like? It is easy to produce such new characters by environmental action, and it is easy to find in certain cultures individuals that present unusual features. Specimens with altered form, with new appendages, with differently arranged parts, are not very rare. Many of those found in natural cultures correspond in appearance to what we might expect of a *mutation.*

Will such untypical characters reappear in the progeny, so that we shall get a race with the new characteristic?

Examination of a large number of cases in Paramecium shows that these untypical characters are never reproduced in the young. Sometimes such a thing as an appendage may pass bodily to one of the progeny, just as a parasite clinging to the outer surface might do; but there is no multiplication of such a character; no tendency to produce a race bearing it. The young reappear in the form typical for the race, without regard to the individual peculiarities of the parent.[4]

What is produced in the new generation therefore depends on the fundamental constitution of the race, not on the accidental form of the parent. Again the analogy

[4] For many examples of this, with figures, see the first of the papers already referred to.

with crystallization forces itself on us. The characteristic form of crystals is easily changed; by filing off the angles we might convert a large number of pyramidal crystals into the quite new form of cubes. But if we dissolve these and allow them to recrystallize, we obtain, not cubes, like the parents, but the original crystalline form characteristic for that particular chemical compound.

If we should modify the chemical constitution of the substance, it would then crystallize in new shapes. If we could modify the fundamental constitution of the organism we should probably find it likewise appearing in new forms. Whether this occurs at times in unicellular organisms we shall ask later. But it is important to grasp the fact that it does not occur often nor easily; that the ordinary activities of life do not observably bring it about; that the mere presence of a new character in the parent has no evident tendency to produce such a result. Many of the untypical forms found in Paramecium were such as one might imagine due to an alteration in the fundamental constitution of the race (a mutation?), but the new characteristic was not reproduced in the progeny.

But besides the untypical or "abnormal" characters of certain individuals, there are the common differences among individuals that are fully "normal." In the Protozoa, as in all organisms, differences in size and proportion among differing individuals are common; *variation* is the rule here as everywhere. We must then examine these differences, under the question already set forth: What characters are produced anew in reproduction? Will the progeny produce anew these diversities of the parents, in such a way that from large parents arise large progeny, from small parents small progeny, from intermediate parents intermediate progeny?

In Paramecium we find individuals differing greatly in size. From a "wild" lot of Paramecia we isolate such differing individuals and propagate from them, all under

the same conditions. We find that many of these differences *are* inherited; from large individuals we get large races; from small individuals small ones. We find, then, that Paramecium consists of many races, differing from each other in mean size slightly but constantly. Eight of these different races were isolated and propagated for hundreds of generations; some were carried through several complete "life cycles." Each such race consisted of specimens all derived from a single parent individual. Unquestionably many other races exist, that could be isolated by proper means.

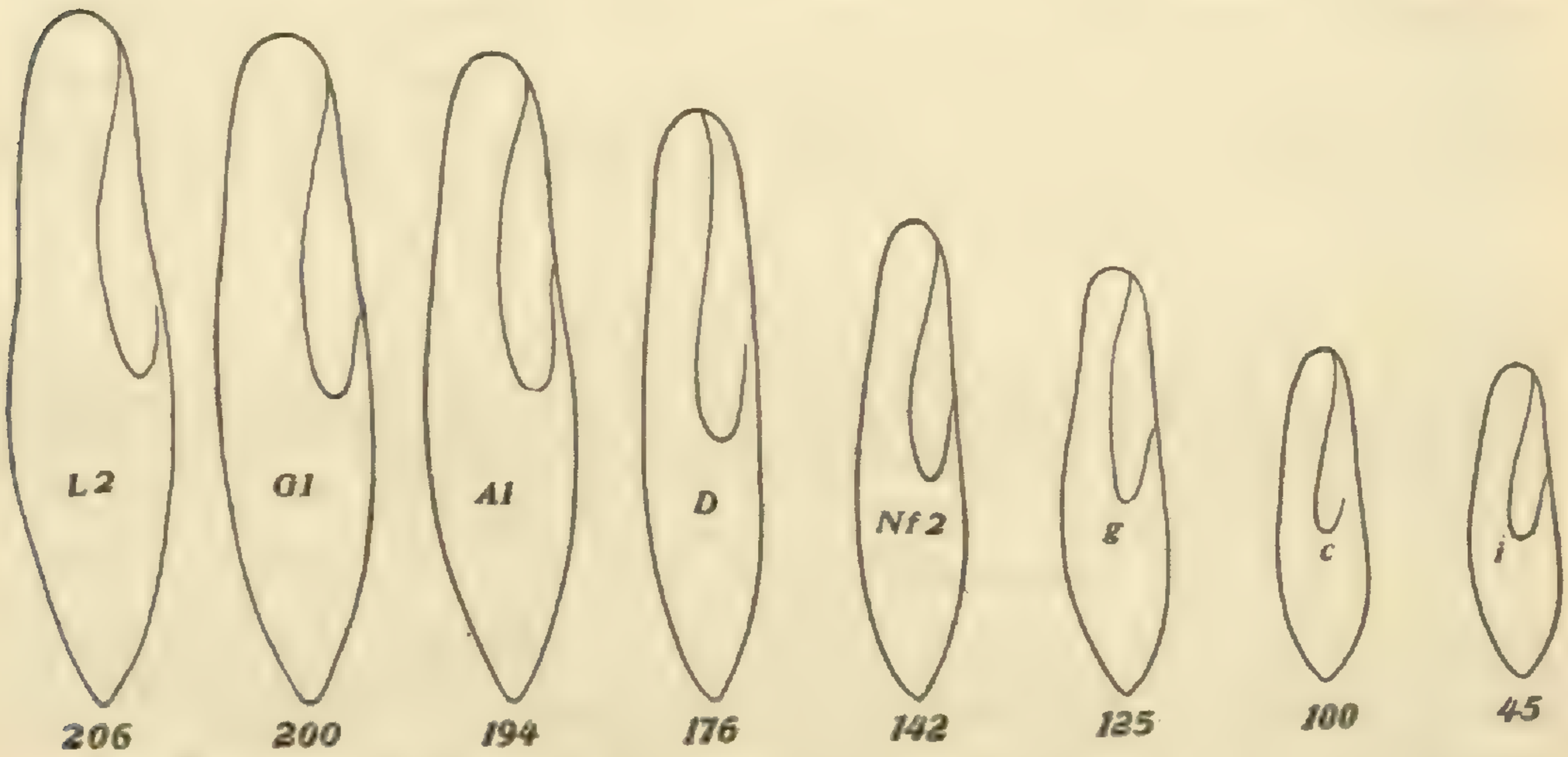


FIG. 3. Diagram showing the relative mean lengths of the eight different races of Paramecium that were isolated. The magnification is about 340 diameters. The actual mean length of each race is given in microns below the corresponding outline.

Fig. 3 is a diagram showing the relative mean lengths of the eight races isolated, as determined by measuring at intervals lots of 100 or more individuals of each race. The mean length for any race is constant under given conditions. The differences between adjacent races are very slight; thus, between the races *c* and *i* of the diagram the difference in mean length was but five to seven microns or .00028 inch. For measuring such constant differences between races even the "fourth decimal place of the biometrician," so heavily contemned of late, would seem to be required. This gives us something of a measure of the minuteness of the steps by which evolu-

tion may occur, if we hold that one of these races has arisen from another.

We find then that by selection we can isolate many races of different mean size, and that the relative mean size is inherited in each race.

But another fact of equal importance comes forth. Within each race (derived from a single parent) the size of the different component individuals varies extremely. The largest specimens of a given race are more than twice as long as the smallest specimens, and every intermediate dimension occurs. We may therefore represent the composition of a single race by the diagram of Fig. 4. These

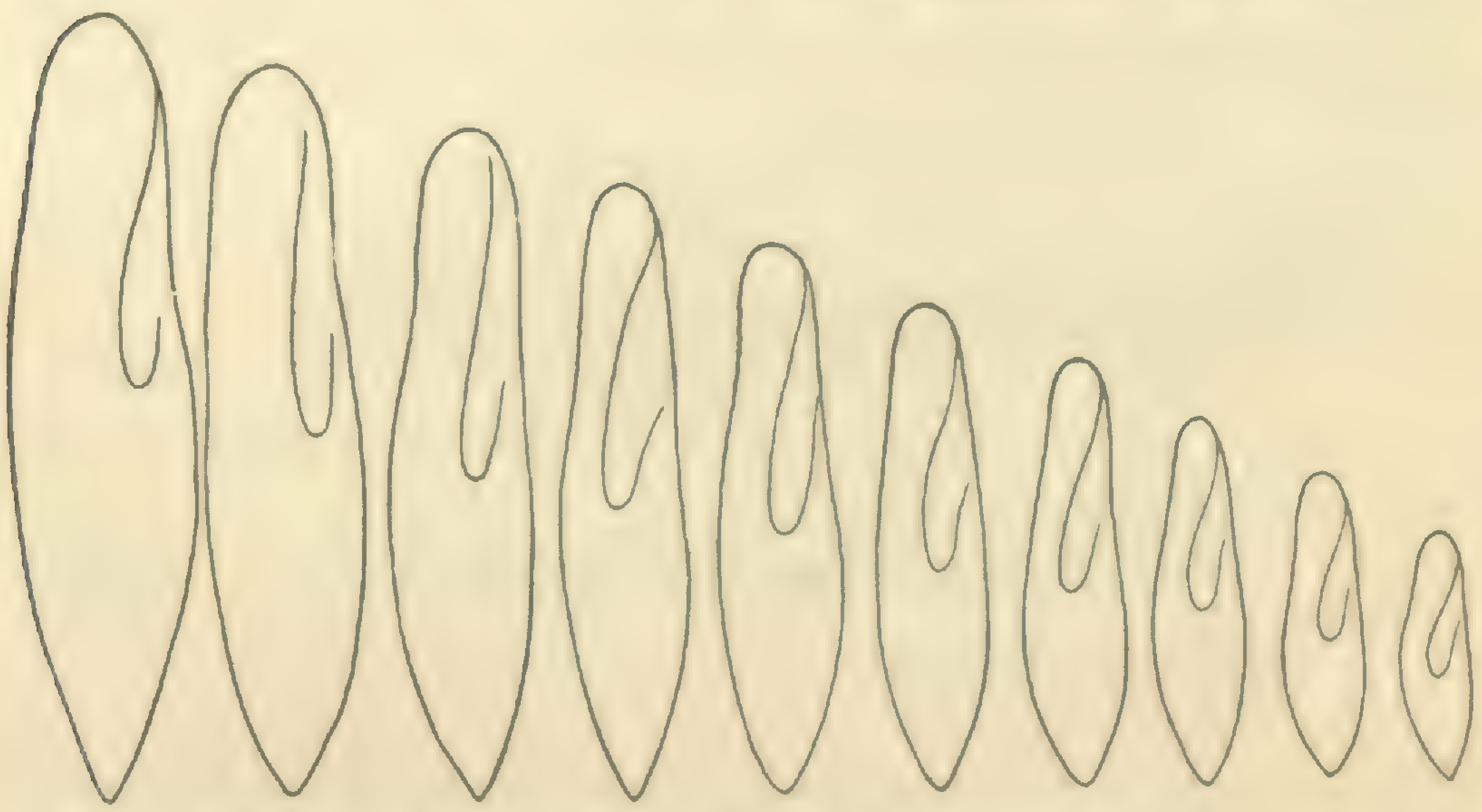


FIG. 4. Diagram of a single race, showing the variations in the size of the individuals. The race represented is *D* of Fig. 3, and the magnification is the same as in Fig. 3 (340 diameters). The individuals vary from 80 to 256 microns in length.

differences in size are due to growth, to amount of nutrition, and to other environmental conditions; a detailed analysis of the action of these factors is given in the second of the two papers above referred to.

Now we come to the most important point. Are the varying sizes within the single race inherited? Will large specimens produce large progeny, small ones small progeny, so that from a single race we can get several, of differing sizes? And can we by repeated selections of

the largest individuals for breeding steadily increase the mean size of a race?

Breeding from the extreme specimens—the largest and smallest—of a single race, we get several hundred individuals from each. *Both produce progeny of the same mean size.* Each produces a whole series of varying individuals, just like the original racial series (Fig. 4); the series produced by the largest individual is exactly like that produced by the smallest, or by any other. The differences between the individuals within such a series are due to growth and environment. Such differences are not inherited: *the race breeds true,* without regard to the peculiarities of the individual parent. A great number of such breeding experiments were carried out, in which selection was continued for many generations, but the results were invariably the same. *Selection within the pure race is of no effect on the size.*

Furthermore, marked differences in the parents due to different environments become quickly equalized in the progeny when the environments are made the same. Thus environmental effects are not inherited. Neither selection nor environmental action changes the size of the pure race.

Thus in our study of the "normal" variations we come to the same result as in our previous study of abnormalities, new characters, apparent mutations, and the like. What is produced in inheritance depends, not on the evident external features of the parent cell, but on the fundamental constitution of the race. Each race has its own peculiar constitution, and under different conditions this same constitution gives rise to various sizes and forms, producing thus the variations within a race, illustrated in Fig. 4. But all these different individuals of a race are potentially the same; at the same age and under the same conditions throughout, all would be alike.

Now consider again the species as a whole: in this

case Paramecium (*aurelia* or *caudatum* or both).[5] We have found it made up in the way indicated in Fig. 5. It consists of a series of many races, differing in mean size; while each race is made up of a series of individuals,

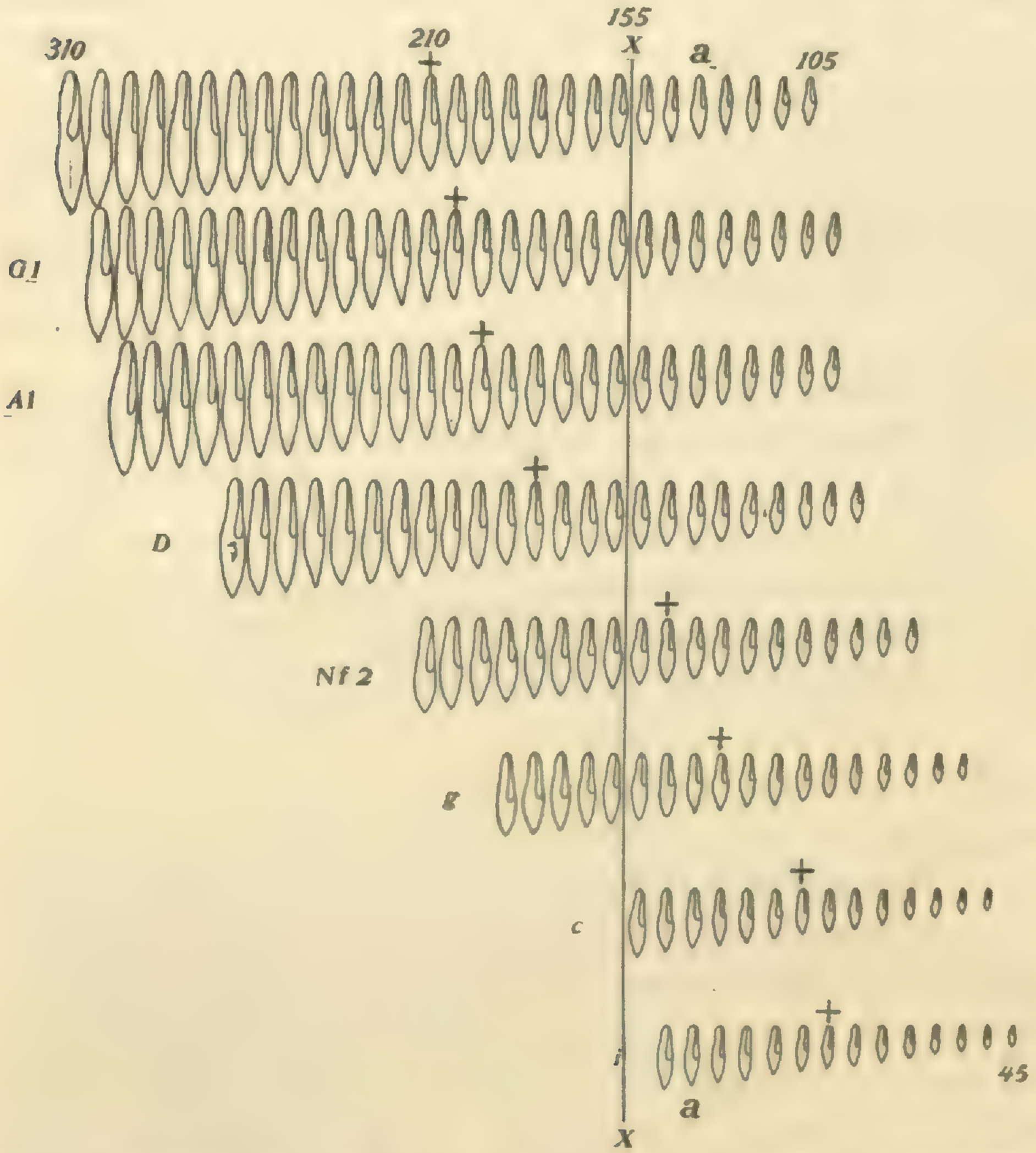


FIG. 5. Diagram of the species of Paramecium, as made up of the eight different races of Fig. 3. Each horizontal row represents a single race. The individual showing the mean size in each race is indicated by a cross placed above it. The mean of the entire lot is shown at *x*–*x*. The numbers show the measurements in microns. The magnification is about 43 diameters.

that are of varying size, though potentially alike. Reference to this diagram will help to understand certain fundamental facts of variation, heredity and the effects of selection in these organisms.

[5] For a discussion of the species question in Paramecium see the second of the original papers, pp. 498–500.

As the diagram shows, individuals of the same size are found in many different races. An individual of the size shown at *a* might belong to any one of the eight races. Thus from individuals of the same size we may get many different results in breeding. Similarly, individuals of very different size (as the extremes of any horizontal series) may produce progeny of identically the same character. We can not tell by its external characters to what race a specimen belongs; breeding is the only test. In higher organisms, as is well known, we often find a similar state of affairs.

How will selection act on such a complex species? As we have seen, selection within a single race is without effect. But if we make selections among the individuals of a mixed collection of races, such as Fig. 5 shows, we reach most instructive results. By making our selections in the proper way, we for a time make steady progress toward a certain goal. We will suppose that we do not know of the existence of these races; this is the case with most experiments in selection. From the species as a whole, as shown in Fig. 5, we will select for increased size. Let us follow the old plan of selecting many individuals showing the desired character; we will preserve all specimens above the mean size of the entire collection. That is, we divide the collection at $x - x$ rejecting all those to the right. By so doing it is evident that we exclude all specimens of the two smallest races *c* and *i*, while preserving the majority of the specimens of the larger races. Allowing these to propagate, we of course get a mixture of the remaining larger races; hence the mean size of the whole collection will be greater than at first. Selecting again those above the mean size of this lot, we drop out another small race, and the mean of the collection as a whole again rises a little. We are making good progress in the improvement of our species. By taking successive steps of this character, dropping out the smaller races, first partly, then completely, one after another, we can for a long time continue to improve by

selection. But finally we reach a stage in which all but the largest race have been excluded. Thereafter we can make no farther progress. In vain we choose for breeding the largest specimens of the lot; all belong to the same race, so that all produce the same progeny. Selection has come to the end of its action.

It is well known that this is a course of events commonly observed in selective breeding. Improvement occurs for a time, then stops. We might have produced the final result at once, in our infusoria, by merely isolating at the first selection the largest individual of the entire lot; its progeny would have produced at once a pure race of the largest size attainable. Selection here consists simply in isolating already existing races; it produces nothing new.

Thus the facts in Paramecium furnish an excellent illustration, in the simplest possible form, of the principles of breeding for improvement so convincingly set forth in de Vries's recent work on plant breeding, and in his other writings.

It is well known that in inheritance extremely marked parental characters appear less marked in the progeny; the progeny of extreme parents are on the whole nearer the mean than were the parents. This fact is spoken of as regression. The reason for this is clear in such a collection as Fig. 5. Suppose we breed from the very largest specimens of the entire collection. These are the largest individuals of the largest race. They produce, as we have seen, like any other specimens of that race, progeny of merely the mean size for that race. The progeny will then of course be on the average smaller than their parents, but they will be above the mean size of the species as a whole, since they belong to the largest race. Thus "regression is not complete"; the progeny diverge from the parents toward the general mean of the species, but do not reach it. If however we consider a single pure race alone (Fig. 4), and breed from the ex-

tremes, then "regression is complete," since the progeny are of the mean size for the race as a whole.

Work with "pure lines"—where no intercrossing of races or individuals occurs—is possible with but few organisms, and little of it has been done. In the few investigations carried on in this way, the same conditions have been found that we have set forth above for Paramecium. They were first shown by Johannsen[6] to hold for beans and barley, and later by Elise Hanel for Hydra.[7] The fact that there exist diverse races, tending to breed true, has of course been shown for many species, but in most cases it is difficult to maintain pure lines, and thus to absolutely demonstrate the relations above set forth, as has been done for beans, barley, Hydra and Paramecium. In the Protozoa it has of course been possible to carry the work through an immensely greater number of generations than in many celled organisms. The extremely important work of Barber[8] has shown the same condition of affairs to exist in yeast and bacteria, though with certain additional factors to be mentioned later.

When we deal with organisms that continually intercross, the conditions of course become immensely complex. Each individual represents, as it were, many diverse lines, whose appearance and disappearance in the hide-and-seek way characteristic of Mendelian inheritance makes interpretation extremely difficult. There is not wanting evidence that the same principles are at work even here; that the results of the study of "pure lines" give the clue by the aid of which the more complex results of selection in biparental inheritance may be unraveled. If this is the case, then selection would act even here also by isolating diversities that already exist, not by producing diversities. There are of course some not

[6] Johannsen, W., "Erblichkeit in Populationen und in reinen Linien," 68 pp., Jena, 1903.

[7] Hanel, Elise, "Vererbung bei ungeschlechtlicher Fortpflanzung von *Hydra grisea*," *Jenaische Zeitschr.*, 43, 1907, pp. 321–372.

[8] Barber, M. A., "On Heredity in Certain Micro-organisms," *The Kansas University Science Bulletin*, 4, 1907, 1–48, pl. 1–4.

yet thoroughly analyzed facts that are difficult to interpret on this basis, so that its general adequacy remains to be determined.

The work with Protozoa emphasizes further certain important points regarding *variations*. The interest of studies in variation lies mainly in the assumption that the variations are heritable, supplying material for selection and evolution; this assumption is openly or tacitly made in most work on the subject. Yet when we actually determine how far this is true, we find (as we have seen) that in a pure race of infusoria *all* the differences between individuals are environmental and without significance in inheritance. If we study these variations by biometric methods and laboriously work out numerical coefficients of variation (as the author has done on a large scale in his original paper) we acquire data which are perhaps not without some sort of interest, but which have no bearing on inheritance or selection or evolution. The "standard deviation" and "coefficient of variation" express in a pure race mere temporary conditions, of no consequence in heredity. If we could make all conditions of growth and environment the same throughout our pure race, all the evidence indicates that the standard deviation and coefficient of variation would be zero, and this is the positive value of their assistance in determining what shall be the characteristics of the progeny.

Even when we deal with mixtures of diverse races the coefficient of variation is, as a rule, mainly determined by differences due to growth and environment. "Wild" cultures of Paramecium, consisting of many races, may not give higher coefficients of variation than those obtained from pure races. The coefficient of variation is then by no means an index to the permanent heritable differentiations in a collection; its value may be high when there are no such differentiations, or low when such differentiations exist. The important question for all such work is: What diversities are heritable, what are not? This is an experimental question, and the rôle of statis-

tics in answering it is a most subordinate one. When an author deals in standard deviations and coefficients of variation, the first question the reader should ask is: Has the author determined what part of the diversities thus measured have any bearing on heredity? They may have absolutely none.

Thus the mere fact that observable variations exist between individuals can not properly be appealed to as furnishing material for selection and evolution, as has been so generally done. Most such variations have in the organisms studied absolutely no bearing on the evolutionary process, and there seems little doubt but that this is true for organisms in general.

Illustrations of the practical bearing of these points may be found without departing from the particular organism with which we are dealing. It has been shown that the two products of the division of a single individual Paramecium often differ in size at a given time, so that "variation" occurs in non-sexual as well as in sexual reproduction.[9] But these "variations" are mere temporary fluctuations, without effect in heredity, so that their relation to evolution is *nil*. Again, Pearl[10] showed that conjugants are less variable than non-conjugants. This is true even within the limits of a single race, as I can confirm from extensive studies. But all the variations in such a case, both in the conjugants and non-conjugants, are purely temporary matters, without effect on posterity; so far as evolution or heredity or selection goes they can be left quite out of account.[11]

Comparative studies have often been made of the variability of higher animals under different methods of reproduction, under different conditions, etc.; the varia-

[9] Simpson, J. Y., "The Relation of Binary Fission to Variation," *Biometrika*, 1, 1902, 400–404. Pearson, K., "Note on Dr. Simpson's Memoir on *Paramecium caudatum*," *Biometrika*, 1, 1902, 404–407.

[10] Pearl, R., "A Biometrical Study of Conjugation in Paramecium," *Biometrika*, 5, 1907, 213–297.

[11] This of course is no criticism of Pearl's paper, which is one of the foundational ones for this line of work. When different races are present, the less variability of the conjugants is of the greatest significance.

bility of parthenogenetic generations has been compared with that of sexual generations, and the like. These have no meaning for evolutionary questions unless we know whether any of the diversities are heritable. In general, it would appear that most observed variations are *not* heritable.

Perhaps more important even than the distinction between temporary modifications and really heritable differences is another point regarding "variations." Even leaving aside the temporary modifications, much discussion of variation assumes that the word implies an actual *change* from one condition to another. This is obviously a very different matter from mere observance of two different conditions in different individuals. If our object is to discover how far we have actually observed evolution *taking place*, the distinction between variation as an active change and variation as an existing condition (of permanent differentiation between two races) is absolutely fundamental. Evidently, observation of the mere fact that permanent differentiations exist between races is a totally different matter from observation of the changes by which evolution occurs; it is compatible with almost any theory of the origin of diversities; for example, with that of special creation. As a matter of fact, do we find the existing races changing or permanent? What light does our study of variations throw on this?

In Paramecium, in the extensive study of many races for hundreds of generations by exact statistical and experimental methods, *not one single instance was observed of variation in the sense of an actual change in a race.* In the detailed paper, coefficients of variation are given almost by the hundred, and permanent diversities of race are registered minutely and in numbers. But these mean nothing so far as real change in any race is concerned. So far as the evidence goes, every race was essentially the same throughout the work, and may have been the same for unnumbered ages before.

For clear thinking it is of the greatest importance to distinguish variation as a process from variation as an existing static condition of diversity. If this distinction is not made, we may delude ourselves into thinking we have seen evolution occurring, when all we have seen is the complexity that induces us to invent the theory of evolution. The difference is just the difference between seeing a problem, and seeing its solution; between asking a question and answering it.

But is there indeed no evidence that actual racial changes occur in unicellular forms? On this point we have the extremely important work of Barber.[11] Barber was the first to undertake in bacteria and yeasts the study of "pure lines"—of races derived entirely from a single individual. In general his results were the same as those set forth above for Paramecium. Many races of yeasts and bacteria exist, and these races are constant (with the exceptions to be noted). Environmental effects were not inherited, and long continued selection was of no effect in changing such a race. Barber studied also unusual individuals; he found, just as I have set forth above for Paramecium, that their peculiarities were, as a rule, not inherited. But he did find a few cases of peculiar individuals *within a pure race,* that transmitted their peculiarities to their descendants. Here we have then actual changes in a race; variations in the dynamic sense. In this way there were produced races of yeasts having cells of a different form; races of bacteria composed of longer rods than the parents. But such cases were *extremely rare.* Variations that perpetuate themselves were found only in one individual among thousands. Barber's work goes as strongly as my own against the significance of the common variations among individuals—such variations as are measured by the coefficient of variation—for heredity or evolution.

To recapitulate, we find that the unicellular organisms are made up of numerous races, differing minutely but

[11] *Loc. cit.*

constantly. The individuals of any race vary much among themselves, but these differences are matters of growth and environment, and are not inherited. What is produced in reproduction depends on the fundamental constitution of the race, not on the peculiarities of the individual parent. The fundamental constitution of the race is resistant to all sorts of influences; it changes only in excessively rare instances, and for unknown causes; in a study of thousands of individuals of Paramecium, through hundreds of generations, hardly a single case of such change was observed.[12] Most differences between individuals are purely temporary and without significance in inheritance; the others are permanent diversities between constant races. Systematic and continued selection is without effect in a pure race, and in a mixture of races its effect consists in isolating the existing races, not in producing anything new.

To give in brief an account of the general results of extensive work, it is necessary to make definite statements, and to omit conditions, exceptions and qualifications. This the reader is asked to remember; the details may be found in the original papers. The results are based on study and measurements of more than 10,000 individuals of Paramecium, kept under experimental conditions for many generations. But science is essentially incomplete and its results at any time are not final. The author expects to make strenuous attempts to overthrow the generality of some of the results set forth.

[12] A single doubtful case is described in the first of the author's two papers: certain individuals of a race acquired a hereditary tendency to remain united after fission, while others did not show this tendency, or showed it less strongly.

THE COLOR SENSE OF THE HONEY-BEE: IS CONSPICUOUSNESS AN ADVANTAGE TO FLOWERS?

JOHN H. LOVELL

In 1895, Professor Felix Plateau, of the University of Ghent, began the publication of a long series of papers, in which he asserted that Hermann Müller, in formulating his theory of the evolution and use of floral colors, had been misled by a too vivid imagination; and that anthophilous insects are attracted chiefly by odor. In a list of his papers prepared by himself and now before me Plateau states that his latest contribution, entitled Les insects et la couleur des fleurs,[1] contains a "summary of the whole." The conclusions of many years of patient research are given at the close of this paper as follows:

> "In the relations between the insect fertilizers and entomophilous flowers, the more or less bright coloration of the floral organs has not the preponderating rôle which Sprengel, H. Müller and their numerous adherents have attributed to them. All the flowers in nature might be as green as the leaves without their fertilization being compromised. The sense of smell so well developed among most insects far from being a secondary factor is probably the principal sense which discovers to them the flowers containing pollen and nectar."

By fertilization Plateau doubtless means pollination, for fertilization is an entirely distinct phenomenon, often not occurring until many months after the pollen has been placed upon the stigma. Plateau's conclusions have not met with general acceptance; and in some instances, as he himself naïvely remarks, have been criticized in a "merciless manner."

Florœcology is, however, greatly indebted to him not only for many very interesting observations and experi-

[1] Plateau, F. Les insects et la couleur des fleurs. *L'Année Psychologique*, 13, 67–79, 1907.

ments, but also for insisting that the whole subject of the relations of insects to the colors of flowers should be re-examined and tested experimentally. With the exception of the criticisms of Bonnier, in 1879, Müller's doctrine had remained unquestioned, for no other theory of the significance of brilliant floral leaves is so satisfactory as that they serve as signals or flags to attract the attention of anthophilous visitors. It is well to recall that the great authority, which has been attached to the name of Müller, rests on innumerable observations and collections, which were continued up to the morning of his sudden death from a pulmonary complaint while studying the flowers of the Tyrol. He is still justly regarded as the foremost of florœcologists. Says his biographer Ludwig:

> "He is not dead, he lives and will live so long as a flower enraptures the eye of an investigator. His bright spirit will live on and, we hope, like that of his teacher and friend Darwin long be a light on the way to truth in the heart of nature."[2]

Plateau's first paper dealt chiefly with the concealment of the flowers of the dahlia with green leaves; and his second, which appeared in the following year, with the removal of petals. In the last-named communication he describes how he removed the larger part of the corolla of *Digitalis purpurea, Lobelia erinus, Œnothera biennis, Ipomœa purpurea, Delphinium ajacis,* and *Antirrhinum majus;* and with the exception of *A. majus* found that the inconspicuous stumps were visited by insects almost as frequently as the unmutilated flowers.[3] He, therefore, concluded that neither the color nor the form was important, and that insects were attracted by the fragrance alone. I shall again refer to these experiments after relating my own, which gave very decisive results diametrically opposed to those of Plateau.

[2] Ludwig, F. Das Leben und Wirken Professor Dr. Hermann Müller's. *Botanisches Centralblatt,* 17, 404, 1884.

[3] Plateau, F. Comment les fleurs attirent les insects, II. *Bul. Acad. roy., Bruxelles,* 32, 504–34, 1896. I have not been able to obtain this paper, the reprints being exhausted. The experiments are described, apparently with sufficient detail, in Knuth's Handbook of Flower Pollination, and it is upon this account that I have depended.

To determine the influence of the petals of the common pear, *Pyrus communis*, upon the visits of the honey-bee, *Apis mellifera* L., a medium-sized tree in full bloom was selected for observation. The day was clear, warm and calm, the bees were numerous and no other insects were present.

A cluster of seven blossoms near the end of a branch was watched for fifteen minutes and received eight visits of the honeybee. The petals were now all removed and it was observed for a second quarter of an hour. Though a number of bees flew near by, it received not a single visit. During a third fifteen minutes there were two visits, due in part to association, for the bees came from other blossoms on the same tree, which had proved the first source of attraction.

Two other clusters of flowers, growing side by side but nearer the bole of the tree, consisting each of eight flowers, were observed for fifteen minutes and sixteen separate visits of the honeybee were noted The petals of one of these clusters were now removed. During fifteen minutes the adjacent cluster, which still retained its petals, received eleven visits, while not one was made to the cluster without petals. In one instance a bee hovered over it but did not alight.

These results were much more conclusive than I had expected; for, in the second experience, it might have been supposed that the odor exhaled by the evaporating nectar of the denuded blossoms would have attracted the bees, which were only an inch or two distant; but their movements were evidently determined almost entirely by the presence of the petals.

On a warm pleasant morning in August at 11:30 o'clock, (A.M., I selected for experiment two groups of flowers belonging to *Borago officinalis*, or the common borage. They were distant apart about six inches; one contained five flowers; the other, which was at a little higher elevation, contained four flowers. They were both watched for ten minutes. The first received fifteen visits from

the honey-bee, the second thirteen visits. The location of my apiary not far away furnished a large and continuous supply of visitors. The rotate corollas, together with the cone of black anthers, the stamens being attached to the base of the petals, were now removed from the five flowers of the first group. There remained the green calyx, the pistil, and the green disc surrounding it which secretes the nectar. The two groups were now observed for a second ten minutes, the first received no visits, the second seven visits from the domestic bee as previously. Once a bee hovered around the denuded flowers of the first group but failed to alight. The much smaller number of visits made to group number two during the second interval may in part have been due to the less conspicuousness of the whole patch of flowers. There were scattered upon the ground many partially withered corollas and twice a bee was seen to fly down toward them. With a lens of twenty diameters I examined three of the defoliated blossoms and in two of them found eight or nine small drops of nectar, so that had a bee alighted upon them it would have been richly rewarded for its discernment. The flowers possessed no perceptible odor. Three points in the second part of this experiment should be carefully noted; first, that the flowers from which the corollas had been removed, though they contained an abundance of nectar, received no visits; second, that the flowers left complete received a much less number of visits than during the first interval; third, that the bees were attracted by the wilting corollas lying upon the ground.

On August 14, I made the following experiment upon a staminate flower of the garden squash, *Cucurbita maxima*. The weather was clear and warm. During an observation of ten minutes it received twelve visits, eight of which were made by honey-bees and four by workers of *Bombus terricola* Kirby. The perianth was then removed close to the cup-shaped reservoir, but the denuded flower with its prominent club of stamens and yellowish disc was still

a conspicuous object though much less so than before. It was watched for a second ten minutes and received only one visit, from a bumblebee (*Bombus terricola*). During the first interval no visit was counted that the bee did not enter the corolla and go down to the honey receptacle. Within a few inches of this "stump" and a little lower down there was another squash flower, the corolla of which had wilted and was nearly closed. During the second ten minutes this flower received five visits,[4] two from *B. terricola* and three from honey-bees, though they were unable with a single exception to find an entrance. There can be little doubt that had the corolla been present on the first flower these bees would have entered it.

On the fifteenth, the weather being favorable, the experiments on the flowers of *Cucurbita maxima* were continued. Two flowers, both staminate, growing side by side, their corollas touching, were selected. Number one appeared rather older than number two, which had evidently expanded very recently. Both were observed for ten minutes. Number one received six visits, four from *Bombus terricola*, two from the honey-bee; while number two received thirteen visits, all from bumblebees (*B. terricola*). The fresher condition of this flower probably accounted for the larger number of visits. Both the calyx lobes and the corolla were now cut away from number two, the most attractive flower, leaving only the disc and the monadelphous club of stamens. This was by no means an inconspicuous object, as the yellowish disc is 15 mm. in diameter, and the yellow anthers are over 2 cm. long. The two flowers were watched for ten minutes. No visits were made to number two; but number one received twelve visits, six from honey-bees and six from *B. terricola*. It is evident that the corolla was a great advantage, and that number one suffered in competition with number two, the number of visits to number one greatly increasing when number two was rendered comparatively incon-

[4] The bees alighted upon the corolla and tried to enter it.

spicuous. Shortly after this experiment was completed a honey-bee was seen to visit the decorollated flower of number two; and inserting its tongue through one of the narrow slits in the top of the cup-like receptacle it remained sucking for two minutes, finding evidently an ample quantity of nectar. It then visited flower number one, but its further flight was not followed. A moment or two later a honey-bee was again seen on the nectar receptacle of number two, which was doubtless the same individual, for its subsequent flight was followed and it returned twice afterwards, finding the nectar here more abundant than in the complete flowers. Later a fifth visit was observed, probably by the same bee. There were many more bumblebees present than honey-bees, and the greater capability of the honey-bee in finding the nectar and in making the most of its discovery is noteworthy. During this whole time number one, from which the corolla had not been removed, continued to be frequently visited by bees. The corolla of the squash possesses an agreeable fragrance, but the defoliated flower also exhales a strong though coarser and more weed-like odor. The visits were recorded on the instant they were made.

In these experiments the visitors were not a miscellaneous group of insects belonging to several orders and differing widely in their habits of visiting flowers and, according to Müller, in their color sense; but the flowers of *Pyrus communis* and *Borago officinalis* were visited by *Apis mellifera* alone, and of *Cucurbita maxima* by *Apis mellifera* and *Bombus terricola*, allied species, which are placed by some authors in the same family. The visits were purposive and not ambiguous, as is not infrequently the case with the visits of many diptera and even of the less specialized bees. To the complete flowers the number of visits were numerous and decisive. On the contrary, they ceased almost entirely to the decorollated flowers, though they contained an ample supply of nectar; while at the same time in the control observations made for the purpose of comparison they continued numerous. The

few exceptions may be explained by the odor of the evaporating nectar, and by the tendency of bees to return habitually to a place where they have once obtained food. That the white, blue and yellow corollas were beneficial to the flowers of their respective species does not admit of question. To attribute this advantage to any other cause than conspicuousness would appear to be a perversion of the facts.

Let us again refer to Plateau's experiment with *Digitalis purpurea*. The larger part of the tubular corolla was cut away leaving a cup-shaped stump 1 cm. long, which was visited by two bees, *Bombus terrester* L. and *Anthidium manicatum* L., nearly as frequently as when the flower was complete. Knuth suggests that the nectar now being exposed to the sunshine and wind must evaporate more rapidly, give out a stronger odor, and should attract more insects than when it was concealed at the bottom of the long corolla-tube. As this was not the case, he holds that the uselessness of the bright corolla was not proved. I should explain the continuation of the visits of the two species of bees as follows. A cup-shaped flower 1 cm. long is by no means very inconspicuous *per se*. The bees had already visited these flowers and learned that they contained nectar; and they would come again to the same place in accordance with their well-known custom of returning habitually to a locality where they have once procured food. They would find smaller, more open flowers with perhaps a stronger odor; but that insects with the keen discernment of bees should be greatly deceived by this change is highly improbable. The results observed by Plateau in the excision of the corolla of *Digitalis purpurea* are precisely those which would have been expected. The force of this objection occurred later to Plateau himself in the case of flowers masqued with green leaves, as when he enveloped with the leaves of rhubarb the inflorescence of Heracleum, for he says:

"Or, j'ai effectué en 1895 et 1896, aux débuts de ma longue serie de recherches sur les rapports entre les Insects et les fleurs, des expériences

que l'on n'a certainement pas oubliés et dan lesquelles je constatais de multiples visites d'Insects à des fleurs dont toutes les parties colorées étaient cachées par du feuillage. L'objection que les résultats de ces expériences ancienne étaient précisément et exclusivement dus au souvenir de l'emplacement se présente immédiatement à l'esprit."

"Je reconnais bien volontiers que cette objection frappe juste pour certaines des expériences en question."[5]

But in my experiments with the heads of simple dahlias masqued with grape-leaves, Plateau continues, the memory of a place visited habitually does not wholly explain the behavior of the insect visitors. In some instances he covered up only the disc florets, leaving the ray florets exposed; in others he covered the entire upper face of the capitulum, both ray and disc florets, but not the under side, with green leaves, and both bees and butterflies (species of Bombus, Megachile, Pieris and Vanessa) continued to fly toward the inflorescences and often found the pollen and nectar by creeping under the covering of leaves. Plateau concludes that the rays do not act as signals, and that the form and bright colors of the capitula of dahlias are not an important influence in attracting insects.

These conclusions are disputed by Forel, who in the following interesting experiment shows that bees in their visits to covered dahlia heads are guided by both memory and sight.[6] In a dahlia bed containing forty-three floral heads of different colors he covered up twenty-five with grape-leaves bent around them and fastened with pins. Of four others he covered only the discs, while of one he covered the rays, leaving the disc visible. The bees were so numerous that at times there were two or three to a flower. The bees ceased at once to visit the completely covered heads; they continued, however, to fly to the heads with only the discs covered, though they immediately abandoned them, except in a few instances where

[5] Plateau, F. Note sur l'emploi de recipients en verre. *Bul. Acad. roy., Bruxelles*, No. 12, pp. 741–75, 1906. Vid. pp. 771–2.

[6] Forel, August. Ants and Some Other Insects, translated by William Morton Wheeler. The Open Court Publishing Co., Chicago.

they succeeded in finding the central florets beneath the leaves; but to the dahlia with the disc exposed and the rays covered they continued to fly as usual. But the bees remembered the earlier condition of the dahlia bed and seemed to be seeking the dahlia heads which had so suddenly disappeared. Soon a poorly concealed specimen was detected and visited, then another, and at the end of about three hours the entrances at the side and below were discovered and the hidden flowers were again being visited. Forel says:

> "Plateau, therefore, conducted his experiments in a faulty manner and obtained erroneous results. The bees still saw the Dahlias which he at first incompletely concealed. Then, by the time he had covered them up completely, but only from above, they had already detected the fraud and saw the Dahlias also from the side. Plateau had failed to take into consideration the bees' memory and attention."

To Forel's criticisms published, in 1901, in *Rivista di Biologia Generale*, Plateau has replied in part: That not only bees but numerous diurnal lepidoptera visited the masqued dahlias, and that while it was freely admitted that insects could see the under side of the covered capitula and the radiating form and red or rose color of the floral ligules, yet they were without attractive value, as it was only very rarely that an insect approached the inflorescence of this side.[7] To these statements I will again refer later. His further explanations as well as his assertions that his opinions have in some particulars been misunderstood by Forel are immaterial to the present discussion. But in admitting that the visits of hymenoptera can be partially explained by memory Plateau practically abandons his position so far as his experiments with dahlias are concerned.

Forel, as has already been mentioned, points out that Plateau has attached too little importance to the bee's memory and attention. These are, indeed, qualities more likely to be appreciated by the practical apiarist than the

[7] Plateau, F. Note sur l'emploi de recipients en verre. *Bul. Acad. roy., Bruxelles*, No. 12, pp. 772–75.

entomologist. A single example will suffice to show the strength of the bee's memory for location. During September and the early part of October, while carrying on various observations, I accustomed honey-bees to visit the window of my library for honey and sugar syrup, and now nearly a month and a half later, though they have not been fed since, they still continue to return whenever warmer weather permits. I have little doubt that when the winter is past and they resume flight in April, as in the experience of Huber, they will come again. I shall certainly expect them.

The great perseverance and power of observation exhibited by bees, when searching for nectar in a locality where they have previously procured it, is likewise well illustrated by Forel's experiment. For more than three hours they continued to look for the missing dahlia flowers, until finally they detected a way to reach them under the leaves. This acuteness of sense is also well shown in the following experiment, which I performed on October 6 after most of the natural flowers had perished.[8]

I accustomed a number of bees to visit a red glass slide, 3 inches long by 1 inch wide, on the center of which was a small quantity of honey The slide was placed in the sunlight on the top of a white box about two feet high. A second white box was then placed fifteen feet from the first and to this the red slide was removed. A bee found the honey at the end of six minutes and a few seconds later another came. In ten minutes there were four bees. During this interval the bees were continually flying around the first white box. I now removed the second white box but left the first undisturbed. An hour later

[8] It is instructive to compare this experiment with one described by Lubbock, where the attention of the bees was preoccupied. "I placed a saucer of honey," he says, "close to some forget-me-nots, on which bees were numerous and busy; yet from 10 A.M. till 6 only one went to the honey." ("Ants, Bees and Wasps," p. 280.) "Attention is surprisingly developed in insects," says Forel, "often taking on an obsessional character and being difficult to divert." ("Ants and Some Other Insects," translated by William Morton Wheeler, p. 21.)

I replaced the second white box, but for the red slide I substituted a plain glass one. A bee found it almost immediately, probably one of the earlier visitors. The slide was now carried to a third position and placed upon an unpainted support fifteen feet from each of the white boxes, the three stations forming the angles of an equilateral triangle. Here it was soon found by two bees. The plain glass slide was then placed on the grass in the center of the triangle, where it was quickly discovered by two bees and a third came a little later. The slide was now placed on the grass fifteen feet outside of the equilateral triangle. It was so inconspicuous that a child, who under my direction approached within a foot of it, failed to see it until a bee alighted in the grass. It required twenty minutes for the bees to find it, and perhaps they would not have done so then had it not been near the route they were pursuing in going back and forth to the hive. It is very evident from this experiment that a force of bees searching for nectar or honey are not easily deceived, but perceive very keenly. The slide was in the sunlight and the attractive influences were the reflected light, the yellow color of the honey (it was golden-rod honey, which is amber-colored), and its odor.

In view of the above observations it can excite no surprise that the bees passed readily under the green leaves which Plateau had pinned on top of the *Dahlia capitula*. The factors by which they were guided were memory and the senses of sight and smell. When the bees returned they found the covered dahlias still in their original position, and though they were not bright colored from above they possessed conspicuousness of size and form; and when the bees in flying about saw the form and color of the rays from beneath and perceived the characteristic odor they recognized promptly the presence of dahlia flowers. Plateau's contention that the form and color of the under side of the capitulum, which was plainly visible, exerted no influence because the insects very rarely approached the head from that side, is without force, for the bees never having found the nectar on the

under side, directed their flight toward the aperture or passageway under the leaves, remembering that the nectar was obtained from the disc flowers. It is not justifiable, says Kienitz-Gerloff, to infer that the color of uncovered flowers plays no part in attracting insects, because when they are covered the odor continues attractive.[9]

Plateau repeatedly mentions that the covered dahlia heads were visited by species of Vanessa and Pieris as well as by bees; but while it is admitted that the mental attributes of bees exceed those of lepidoptera, yet the conclusion that the latter were influenced by odor alone is unwarranted. When a butterfly thrust its proboscis beneath the leaves it showed perception of the form of the inflorescence and memory of the location of the nectar. In the following experience the butterflies exhibited keener powers of observation than some of the less specialized hymenoptera. The flowers of *Iris versicolor* are pollinated by bees; and the nectar, which is secreted at the base of the sepals, is protected by the arched petaloid styles, so that it can not be obtained by butterflies in the legitimate way. I have seen *Pamphila mystic* Scudd. standing on the ovary below the perianth and sucking the nectar through the crevice between the sepal and the style; while the larger banded red butterfly, *Limenitis disippus* Godt. obtains the nectar in the same way from above. On the other hand, an hymenopter, which escaped capture, carefully examined the center of two flowers but failed to locate the nectar. There is good reason, then, to infer that the butterflies in Plateau's experiments were influenced by the position and form of the dahlia heads and the color of the rays below as well as by the odor. The criticism of Kienitz-Gerloff is also as applicable here as in the case of bees.

The experiments of Plateau with covered dahlia heads, therefore, were not well adapted for the purpose intended, and afford an insufficient basis for drawing the conclusion that bright coloration is not advantageous to flowers.

[9] Knuth, P. Handbook of Flower Pollination, 1: 205.

VARIATION IN THE NUMBER OF SEEDS PER POD IN THE BROOM, CYTISUS SCOPARIUS

DR. J. ARTHUR HARRIS

CARNEGIE INSTITUTION OF WASHINGTON

WHILE at Wood's Holl in August, 1907, I collected about 100 pods each from a series of 23 bushes of the broom *Cytisus scoparius*. On a vacant lot not far from the Marine Biological Laboratory the plants were growing vigorously, completely covering the space with bushes, many of which were higher than a man's head, and with stalks about an inch in diameter at the base. The material was gathered for an investigation of the relationship between the number of ovules formed and the number of seeds developing per pod. But when the counting was taken up the determination of the number of aborted ovules proved so difficult that I feared the results would be untrustworthy and gave up the project. While working over the data I noticed that Pearson[1] has recorded a series of countings of broom from an English locality, and it has seemed worth while to compare the two lots of material.

Many biologists have held the opinion that changed conditions of life, such as may be supposed to prevail when a species is transferred from one habitat to another, imply an increase in variability. The theories concerning the reason for this phenomenon need not be discussed here. I think the general idea will be familiar to all. I think about the only attempts to determine quantitatively whether there is any increase in the variability of a species when introduced into a new habitat are two studies by Bumpus. He first considered the variability of the egg of the introduced sparrow[2] and concluded that it is decidedly more variable in the United States than in its

[1] Pearson, K., and others, *Phil. Trans. Roy. Soc. Lond.*, A, 197, 335, 1901.

[2] Bumpus, H. C., "The Variations and Mutations of the Introduced Sparrow," Biol. Lect. Mar. Biol. Lab. Wood's Holl, 1896–97, 1–15.

native country. In judging Bumpus's data on the directly measurable characters by the standard deviation instead of the range of variation Pearson[3] concluded that the American egg is not more variable than the English but rather less so when a more representative English series is taken. It is quite impossible to determine from the color and shape appreciations whether Pearson's English or Bumpus's American series is the more variable, but it seems to me upon rereading Bumpus's paper that he makes a very good case for a greater variability in color and shape of the eggs of his American as compared with his English series. However, Pearson's suggestion of a possible change in the color of the egg must be remembered. Vernon[4] considers the American eggs more variable in shape and color.

Bumpus's second attempt to secure data upon this question was with the introduced Littorina.[5] He found from an examination of three English and ten American series, each of about one thousand individuals, that the American shells are much more variable than those from the British Isles. Duncker[6] who has reworked the data to express the variability in terms of the standard deviation and theoretical instead of empirical range agrees with his conclusions.

The results reviewed above indicate that more data on this question are much needed. Although his conclusions were based upon somewhat unsatisfactory statistical methods Professor Bumpus deserves very large credit for his thoroughly pioneer attempts to solve some of the problems of evolution in the only way in which they can be solved—by the collection of pertinent quantitative data. The problem of variation is such a complex one

[3] Pearson, K., "Variation in the Egg of the Sparrow," *Biometrika*, 1, 247–249, 1901.

[4] Vernon, H. M., "Variation in Animals and Plants," New York, 1903.

[5] Bumpus, H. C., "The Variations and Mutations of the Introduced Littorina," *Zool. Bull.*, 1, 247–259, 1898.

[6] Duncker, G., "Bemerkung zu dem Aufsatz von H. C. Bumpus: The Variations and Mutations of the Introduced Littorina," *Biol. Centralbl.*, 18, 569–573, 1898.

and sources of error are so numerous that great stress is not to be laid upon the results of the examination of a single series of material, but all conclusions must be tested repeatedly and on widely dissimilar organisms. The present lot of broom deserves consideration in this connection.

Cytisus is a native of Europe which has been reported from several localities in the United States. Mr. Vinal N. Edwards writes me that he started the colony from which my collection was taken in 1887 when he set out forty small plants which he dug up on Naushorn Island. In 1898 it was all cut down level with the ground when it came up thicker than ever. He thinks it was first planted on Naushorn Island some fifty years ago.

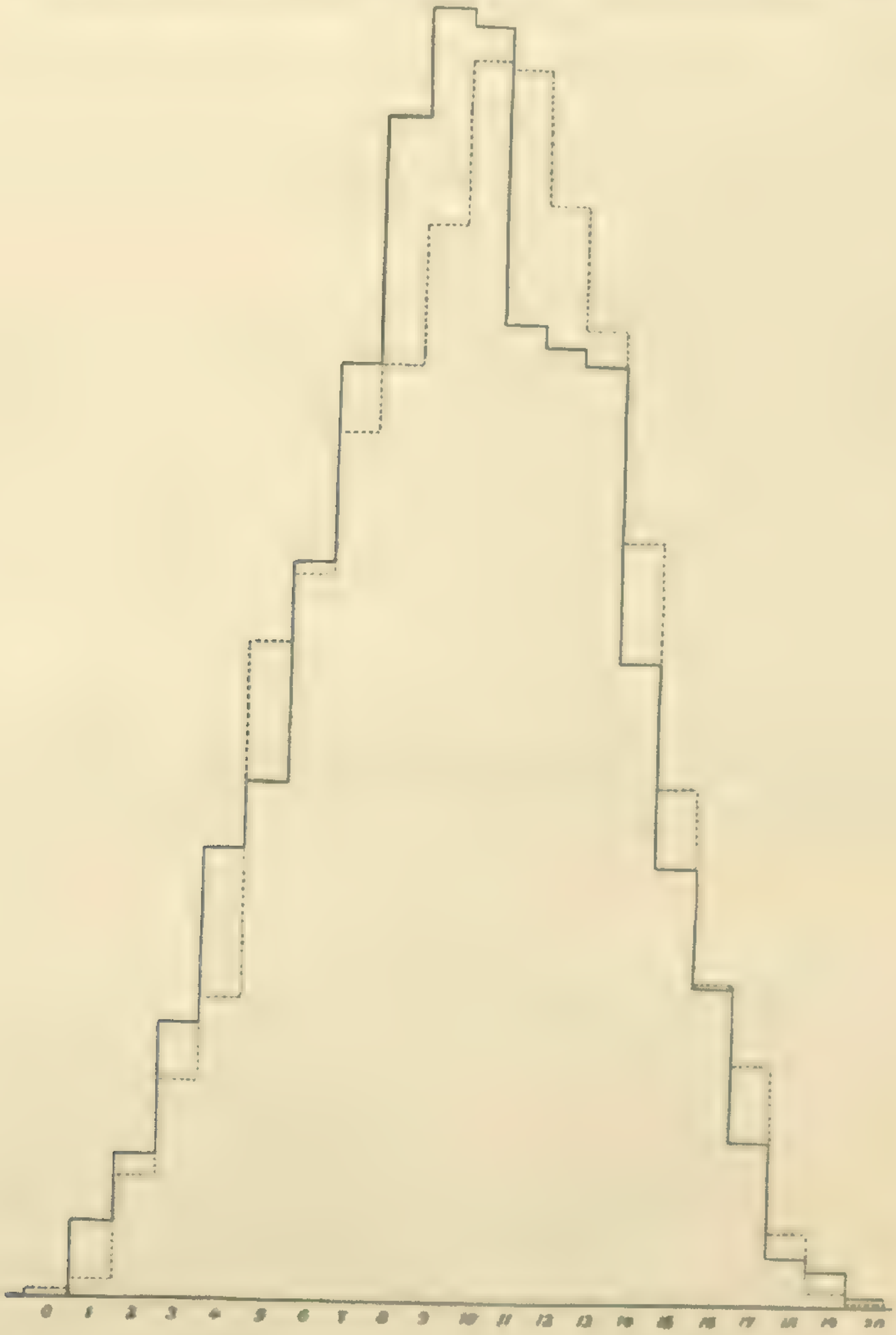
It seems hardly worth while to look farther for the ultimate origin of the colony since we have only a single series of European data for comparison. Several years ago Pearson collected ten pods each from a series of 120 plants at Danby Dale. To render his series readily comparable with my own I have multiplied his frequencies by

TABLE I

VARIATION IN NUMBER OF SEEDS OF BROOM

Seeds per Pod.	Danby Dale, England.	Wood's Holl, Mass.	Difference.
0	—	2	— 2
1	15	4	11
2	28	24	4
3	54	43	11
4	88	59	29
5	101	129	—28
6	144	142	2
7	183	170	13
8	235	183	52
9	254	213	41
10	250	244	6
11	192	242	—50
12	186	216	—30
13	183	190	— 7
14	125	149	—24
15	89	101	—12
16	61	63	— 2
17	32	47	—15
18	9	14	— 5
19	7	3	4
20	2	1	1
Totals	2,239	2,239	

the ratio 2,239/1,200 and placed them beside mine in Table I. The character of the pods is also shown graphically in the diagram where the solid lines represent the English and the dotted lines the American pods.



I think these polygons agree remarkably well. The empirical range is essentially identical. In both cases the highest class is 20. Pearson found no pods with an entire absence of seeds in the 1,200 which he examined, though he suggests that such may exist; I found 2 in the 2,239 of my lot. At first the differences between the frequency of pods in the individual classes, as shown in the fourth column of the table, and graphically in the diagram, seem rather large. But we must remember that two series of countings from the same individual would show many chance differences in their frequencies, and

that neither of the series with which we are dealing is large enough to give very trustworthy results for the frequency of individual grades. We might avoid to some extent the difficulties introduced by the errors of random sampling by graduating the observed frequencies by some satisfactory fitting formula, but it does not seem profitable to take up the labor of curve fitting on the available data. We may, however, calculate the means and variabilities with their probable errors. The constants and their differences appear in Table II.

The means show that the Wood's Holl plants have about three tenths of a seed more per pod than the Danby Dale series. This is to be expected from the diagram where the polygon for the American series is seen to lie a little further to the right than the English. But the difference is only about four times its probable error and so only doubtfully significant even for the samples in hand. I think no one can examine these results and not be convinced that so far as is shown by the physical constants

TABLE II

COMPARISON OF STATISTICAL CONSTANTS OF BROOM

	Average and Probable Error.	Standard Deviation and Probable Error.	Coefficient of Variation.
Danby Dale	9.6425±.0691	3.5466±.0488	36.780
Wood's Holl	9.9982±.0502	3.5236±.0355	35.242
Difference	—.3557±.0854	—.0230±.0603	—1.538

the two collections, one gathered in England and the other in America and counted and reduced by independent observers, are practically identical when we have regard to the probable errors of random sampling. And this notwithstanding the fact that the age of the plants, the number of plants involved, the ancestry of the individuals, and the climatic and soil conditions under which they grew are not taken into consideration or allowed for in any degree! If the constants were based on some character which the qualitative biologist would guess to be little influenced by the environment one might not be surprised at their close agreement; but we are dealing with

a character dependent not merely upon the internal and external factors determining the form of all plant organs, but upon the environmental factors influencing the chances for fertilization as well. Furthermore, it may be noted that we are dealing not with a little variable character, but with one having a coefficient of variation of about thirty five per cent. This is about two or more times the value of the coefficient of variation of the ordinary vegetative characters of plants, but not an extraordinarily high value for seed numbers, as determined from large series of unpublished data.

Summarizing the results of this note, I think we may say that so far as is shown by this one series of material Cytisus is no more variable in the habitat to which it has been very recently introduced than it is in one of its native habitats. As a matter of fact it is slightly, though not significantly, less variable at Wood's Holl than at Danby Dale. Possibly the sensible identity of the variability of the two samples may be due to the small number of individuals which furnished my series of data. These in their turn were probably derived from very few ancestors. I attach no great importance to the results. They simply show that so far as the present material is concerned there is no evidence in favor of the theory that the introduction of a species into a new habitat increases its variability. Possibly some other character than number of seeds per pod would have shown an increased variablity. I use this character merely because I had the data on hand as a by-product of some other work and felt that it would be better to let it contribute its bit of evidence on this problem than to throw it away. Possibly as a fellow biologist remarked when I showed him the closeness of agreement of the constants from the two series the result is "purely accidental." There are many possibilities of error in work of this kind. But until we have a large number of series of quantitative data it will be quite impossible to say whether or not there is anything of value in the theory of an increased variability of "introduced species."

PRESENT PROBLEMS IN PLANT ECOLOGY[1]

The Trend of Ecological Philosophy

PROFESSOR HENRY C. COWLES

University of Chicago

That Schimper was a prophet as well as an ecologist of the first magnitude is well attested by this sentence from the preface to his plant geography:

> The ecology of plant distribution will succeed in opening out new paths on condition only that it leans closely on experimental physiology; thus only will it be possible to sever the study of adaptations from the dilettantism which revels in them, and to free it from anthropomorphic trifling, which has threatened to bring it into complete discredit.

The close interdependence of physiology and ecology is being more and more recognized; this is made manifest by a survey of the titles presented to the botanical meetings year by year. Suggestive among this year's titles are: Bog toxins and their effect upon soils; experimentally induced root-regeneration in Parthenium; the relation of evaporation to the treelessness of prairies; are alpine plants exposed to increased evaporation? Titles such as these would have been quite impossible a few years ago through the failure of ecologists to recognize the fundamental necessity of building their work upon physiological foundations. Quite as fundamental but less fully recognized, especially by many physiologists, is the dependence of physiology upon ecology. The increasing sanity of physiological problems is due in large measure to the wholesome influence of ecology. In the old days when physiology was a mere laboratory science, and therefore artificial, no experimental test could be too

[1] A series of papers presented before the Botanical Society of America at the Baltimore meeting, by invitation of the Council.

bizarre to be applied to plants. A thing never to be lost sight of is that evolution has taken place out of doors, and that the contortions of a puny plant in our illy lighted and gas-ridden laboratories do not solve our most important problems. In recent years no physiological work of greater import has appeared than that from the Desert Laboratory, where the direct stimulus to research has been contributed by the desert itself and its ecological problems.

The developments of the past decade, therefore, make it essential that physiology and ecology break down the barrier erected for them in Madison in 1893, where it was declared that physiology is experimental and ecology observational. The ecologist must experiment in order to resolve a natural complex of factors into its individual elements, while the physiologist must be a student of field conditions, if he wishes to deal sanely with the great problems connected with the evolution of form and behavior. Recognizing, then, the interdependence if not the complete identity of experimental ecology and field physiology, it becomes necessary to consider the underlying philosophy that serves as a motive for all research along these lines. The importance of one's philosophy upon his research can scarcely be overestimated, for it determines the problems to be attacked, the methods to be employed, and, on account of the personal equation, is likely to give some color to the results secured. But it is not necessary that the working theory be true; indeed it is often better that it be most untrue, since it may thus lead to the testing of more theories than might otherwise be employed. The fundamental test of a working theory is that it be that one which will stimulate the maximum of discriminative research. There can be given no better illustration of an unproductive theory than the theory of vitalism. This supposes that there is a fundamental difference between the living and the non-living, hence one would not expect a vitalist to lead in the attempt to create living matter by experiment.

Vitalism, whether true or not, conduces to lethargy, because it assumes a barrier instead of attempting to find if the supposed barrier can be broken down. Thus the mechanistic theory of life is best as a working hypothesis because it leads to decisive experimentation and to the attempt to create living matter, and in this way leads to the solution of many great problems and may some day cause the settlement of that greatest of all problems, the origin of life. On the other hand, vitalism, by assuming to answer the question in a way that transcends the possibility of experimental test, is a hopeless theory and leads to repose and scientific slumber rather than to activity.

While theories of vitalism in whatever form have ever blighted scientific endeavor, they have been especially harmful in ecology. No biologists are brought into closer touch with life than are the ecologists; their whole atmosphere is pregnant with dynamics and the aspect which they have of plants is that of extreme plasticity. The ecologist comes into daily contact with profound changes in plant form and behavior, and he sees ever before him the panorama of succession. What wonder is it that many ecologists have been carried off their feet by vitalism and have dabbled in anthropomorphic similes? And what wonder that, because of this attitude, some of our best biologists have seen naught in ecology but superficial vaporings or scientific nonsense? But the view-point of ecology has been shifting, indeed has largely shifted, and there are reasons for believing that the ecologists are now closer to the problems of to-morrow than many of the other biologists. The rescue of ecology from dilettantism and anthropomorphic trifling, which Schimper so keenly wished for a decade ago, has been essentially realized. It may be of value to outline the steps that have led to the present happy state.

From the beginning one of the greatest of ecological problems has been that of the origin and significance of adaptations. In other days the solution was sought in special creation, one of the most unscientific of all

theories, because altogether subversive of experiment. The entire question was prejudged at the outset. The theory of special creation, however, has not been especially harmful, because it has generally seemed so unlikely as to have received but little support among scientific men. Perhaps the most baneful of all ecological theories has been the Lamarckian theory of direct adaptation. In its day, that is before 1859, it marked a distinct advance, because it was the first significant attempt to displace special creation by something better. The great merit of Lamarckism was the recognition of plasticity, the substitution of a dynamic for a static nature. Had it been generally accepted, it might easily be said to have marked the greatest single step in the advance of scientific thought, but the world was not then ready for dynamic conceptions. The leaven of Laplacian astronomy had scarce begun to work, and the Lyellian geology was as yet unborn.

The evil wrought by Lamarckism is due to its acceptance by modern biologists. It is essentially a vitalistic theory, presupposing that plants and animals have some inherent mysterious power to contravene the ordinary laws of matter. They are supposed to be able to survive hard conditions because able to adapt themselves advantageously. Of course it is clear that those plants which do respond favorably to changing conditions will be most likely to survive, but adaptationists have apparently overlooked the fact that thousands of species must have died because unprovided with an adequate capacity for advantageous response. Their conception of nature is distorted by centering their attention upon those successful plants that appear to have survived because of their adaptations. The depressing effect of the adaptation hypothesis is most obvious in that it has encouraged sterile imaginings as to the advantages of this, that or the other plant structure and has thus discouraged attempts to discover the real facts involved in the origin of such structures.

Evidence against the reality of adaptation in a subjective sense has been accumulating. At first sight the increase of cutin in plants exposed to increasingly xerophytic conditions, or the increased development of air chambers in plants exposed to increasingly hydrophytic conditions look like adaptations, and such changes certainly seem advantageous. However, there are facts that point in another direction. There is no more important source of strength in plants than that afforded by bast and similar mechanical tissues. Yet recent experimenters have failed to get any significant response in the way of great bast development by exposing growing organs to considerable tension. Bast primordia, however, are very plastic and respond readily to changes in moisture. Thus we have in bundles of bast fibers tissues that do not adapt themselves to a demand for tensile strength, although such a response would be highly advantageous; on the other hand, they respond to increased transpiration, although it has not been claimed that bast fibers are of especial value in checking transpiration. Again, increased conduction, whether due to high transpiration or other causes, often results in an increased development of the vascular tract. The advantage of such a modification is at least dubious in xerophytes, but the case is much more striking in such plants as Artemisia, when parasitized by Orobanche. The Artemisia root is stimulated to excessive development by the attack of the parasite, and examination shows that the vascular tract in particular is greatly increased. If this change in the Artemisia root is an adaptation, it is an adaptation for the Orobanche and not for itself, and what adaptationist could expect a plant to be so altruistic as all this? Similar phenomena are seen in fungus and insect galls, and in the cynipid galls in particular, food accumulates in large amount in definite layers around the larval chamber. Can the oak be supposed to be so thoughtful for the insect as to provide it food? Or, if one chooses the other horn of the dilemma, can the insect be supposed to have

learned the habits of the oak, and found just how to tap it? How much more sane it is to regard these and all other plant reactions as brought about through the influence of specific stimuli, treating any advantage that may come (or any disadvantage) as quite incidental to the main problem!

At the present day Lamarckism and adaptation are scarcely as detrimental to ecological thinking as is the misapplication of Natural Selection. The publication of the "Origin of Species" in 1859 influenced biological thought more profoundly than any other work of all history. It compelled the world to accept the doctrine of organic evolution, and it showed most clearly why certain species die and others live. But it shed only a little light on the great questions involved in the evolution of new species. In view of this it seems most unfortunate that the book was entitled "The Origin of Species"; the alternative title commonly printed just beneath in smaller type presents the real thesis of the book: "The Preservation of Favored Races in the Struggle for Life." Perhaps in part because of the title, but more because of Darwin's over-zealous supporters, natural selection has been made a fetish and has been supposed to account for new forms and structures, as well as for their preservation. In other words, it has been erroneously regarded by many as a theory of evolution instead of a means of accounting for the perpetuation or destruction of species previously formed. The theory of natural selection has worked great harm in the ecological study of plant structures. Thorny plants have been supposed to be selected by reason of animal incursion, and such complex things as floral structures have been supposed to be the result of parallel selection on the part of flowers and insects. There is no adequate evidence, experimental or otherwise, for views of this character. Such experimental work as has been done appears to show that the success or failure of a plant rarely depends upon this or that little advantage, upon which natural selection may be supposed to

work, but rather that its perpetuation depends for the most part upon other things than its so-called adaptations. Few more perfect adaptations for their function can be thought of than the digestive glands of insectivorous plants, and yet there is no evidence in support of the idea that such plants have been able to survive by reason of these glands. The evolution of such a complex flower as that of the orchid along lines that are parallel with the evolution of the mouth parts of a special insect requires a nicety of operation that seems staggering, and all the more because the flower, at least, seems to have evolved so far along the lines of zygomorphy as to be a source of disadvantage rather than of advantage, an impossible idea to the natural selectionist. The facts of regeneration show, as pointed out so ably by Morgan, that plants and animals are often in a position to make an instant new reaction to conditions unlike those to which they have ever been accustomed, and that these reactions may or may not be advantageous; in any case, natural selection can have no possible connection with their origin. The trend of the time, especially among botanists, is unmistakably toward the abandonment of natural selection as a theory of evolution, but ecological work is finding a dominant place for it as one of the controlling factors in succession. The student of vegetation dynamics, more, perhaps, than any other, finds displayed before him an incessant struggle for existence; in the changing conditions, the fitness of an old species to remain or of a new species to displace, it is commonly a matter of profound importance in the vegetative change produced.

This is not the place to enter upon a discussion of those evolutionary theories that to-day hold the foremost place. We are awaiting with keen anticipation the noteworthy symposium on evolution that is to make this meeting historic. Suffice it to say that the downfall of the theory of adaptation does not mean the downfall of epigenesis or of extrinsic theories in general. The likelihood of a profound influence of the external world upon the trend

of evolution was never more evident in the past than it is to-day. The work of Klebs has opened up almost limitless possibilities along such lines. The intrinsic theories of evolution, such as orthogenesis and heterogenesis (or mutation) are also vigorously maintained. All such theories, both extrinsic and intrinsic, appear to be in harmony with the present results of ecological research, and the future alone may say whether some or all of these and more are true.

To the working ecologist the necessary consequences of the abandonment of the idea of adaptation and of natural selection as a causative factor are most vital. First and foremost there comes the possibility of disadvantageous trends in evolution. To some extent such tendencies will be checked by the destructive operation of natural selection, so that only such new species as are most fit are likely to survive and have progeny. But in view of the ideas that have generally prevailed in past years, it can not be emphasized too strongly that plants may retain useless structures and even structures that are moderately harmful, and yet live on if they also possess other structures or habits that are sufficiently advantageous. This conception at once relieves ecologists of one of the most arduous of their former duties, the establishment of an advantageous function for every organ, and of a benefit in every function. The chapters on the uses of palisade cells, crystals, poisons, latex and the myriad kinds of hairs are likely to be shorter and less dogmatic in future ecological treatises. Even such organs as stomata are apparently being divested of their erstwhile most important function, the regulation of transpiration.

It has been so long the fashion to regard the various kinds of floral structures as most useful that it may be thought ecological heresy to question their utility. The intimate correlation between the evolution of the insect and the flower was such a pretty story that it seems rude to question it, but do we have any adequate evidence of

advantage in the myriad diversity seen in flowers, much less any advantage great enough to have been of significance in directing to any notable degree the trend of evolution? It is usually assumed that dichogamy, heterostyly, prepotency of foreign pollen, and zygomorphy are advantageous characters because they promote cross pollination or pollination by special insects, but the facts on which such conclusions are based are very slender. There are many plants which are regularly close-pollinated and they seem to succeed as well as others. The Compositæ are often regarded as the highest of the seed plants, and they are of especial interest because they are a group that is ecologically successful as well as morphologically advanced, features that often fail to coincide elsewhere. But the Compositæ show comparatively little zygomorphy or insect selection; as a group they are notably geitonogamous or even autogamous, and yet none of the supposed disadvantages of close pollination are evident. Indeed the massing of flowers in heads and the consequent facilitation of pollination between near-by flowers may be one of the reasons for their great success. But there are reasons for believing that any or all kinds of pollination are vastly inferior to vegetative reproduction in determining the success of a group. The notable success of the grasses and sedges is doubtless due to their rhizomes far more than to their flowers, and in the duckweeds and many aquatics the flower has become almost a negligible quantity. Such considerations make it at least doubtful whether many conspicuous floral structures possess the great advantages in the life of plants that have been commonly ascribed to them.

The conception that plant structures may often have originated quite independently of any important use or function, or even independently of any environmental influence is useful at many points. It explains how there can exist the phenomenon of "over-adaptation," which appears to be exhibited in the orchid flower and in the testa of many xerophytic seeds. It makes possible a new

and seemingly saner ecological classification of plant structures.

The work of Witte seems to show that plant forms may be either obligate or facultative, that is that they may be inherent or may be subject to environmental control. In a xerophytic flora, such as that studied by Witte in Sweden, there are many plants of dwarf habit. Experiment shows that these dwarfs behave very differently in mesophytic conditions. Some develop into tall and luxuriant plants, while others remain as truly dwarf as in xerophytic soil. The dwarfness of the former is facultative, of the latter obligate. The former is clearly a response or reactive xerophyte, owing its form to its surroundings; the latter appears to be an inherent or congenital xerophyte, the cause of whose development is as yet unknown. It is probable that further experiment along these lines will show that many other plant forms apparently identical are most unlike in nature and origin. Time will permit but one further illustration. In mesophytic forests one sometimes finds plants that appear to be xerophytes. A notable example of this is seen in many species of Begonia and Peperomia that grow in the depths of the rain forest. Both in external aspect and in all the details of leaf structure such plants appear xerophytic; it seems almost certain that these plants are congenital xerophytes, species whose xerophytism is stamped upon them to such an extent that age-long exposure to the moisture of the rain forest has not destroyed it. Whether congenital forms in the final analysis differ in any radical degree from reactive forms can not now be told; it may be that all plants are or have been plastic, but it is clear that the recognition of the double possibility in the interpretation of plant structures is at present advantageous.

A minor but necessary matter is that of terminology. One of the unfortunate features about language is that expressions lag behind ideas. Long ago we knew that the heart is not the seat of the emotions, but our language

still retains the old phrases. We continue to speak of the rising and setting of the sun. In like manner we still employ such terms as adaptation, adjustment, accommodation and regulation, although these are vitalistic words which imply that plants and animals can transcend their environment and can contravene the ordinary laws of matter (though it is to be pointed out that the word adaptation is harmless when used objectively). The old-time ecologist was very anthropomorphic and delighted in words derived from φιλέω (I love). Ecological literature is still burdened with such words as xerophile, geophilous and entomophily; particularly objectionable is the word myrmecophily, since it is found that plants merely endure the visits of the ants. Such terms as storage and reserve food appear to imply forethought on the part of the plant and should be abandoned. Words like normal and type are far too freely used, for it can not be emphasized too much that one structure or habit is about as normal or typical as any other. The word function, which is *per se* harmless, has almost come to be a synonym of purpose and may, perhaps, give way largely to rôle. It is not an inconsequential matter that we clothe our ideas with words that are correct and adequate. It is worth the effort, even if we are obliged to substitute a cumbersome though scientific phrase for a euphonious but anthropomorphic word. But of course our language is less important than our thoughts. Our scheme of philosophy is fundamental, for it determines the motive, the scope and the direction of our research. The most blighting of philosophies is that which predicates a maximum of dogma, the most stimulating is that which demands a maximum of experimental test.

DISCUSSION ON PROFESSOR COWLES'S PAPER.

PROFESSOR SHAW: If we should, as Professor Cowles says, discard the word "storage" and, in short, if I understand him correctly, all the words which carry teleological ideas, I should like to inquire what we shall say. What resources of the language shall we use to talk to a class about a starchy tuber and avoid implying purposeful adaptation?

PROFESSOR COWLES: It is a difficult question that Professor Shaw asks, I have been working at that for several years, and I have not all of the answer yet, but I have part of it. We now use the word "response," which I am convinced is expressive of no teleological idea. To speak of a response in the living and non-living will answer nearly all purposes, and is entirely free from teleological ideas. The word "storage" is more difficult to handle; personally I use the word accumulation. Take the word "gall," for instance—oak gall; one would hardly teach his class that an oak gall stores, but to speak of food accumulation of an oak gall is not incorrect.

PROFESSOR CLEMENTS: It seems to me that Professor Cowles puts emphasis on the wrong part of the dilemma. If we change our ideas in the proper direction, it is not at all important what we call them. "Response" implies more of vitalism than adaptation, yet I would adopt the idea and let the word stand.

DR. LIVINGSTON: We sometimes try to cut short our expressions too much, as there is a tendency in all things to adopt shorter expressions instead of long ones, and finally a phrase comes to be a single word, and if the process goes on long enough, a short one. In the present stage of ecology, there is perhaps too much tendency to cut our phrases down to single words before the majority of people who are using the words have yet appreciated what the phrase means, and I am quite agreed with Professor Cowles that we can sometimes find other words, as in the case of accumulation instead of storage, which will express the point; but, I think that in many cases, in order to keep our ideas clear, so that elementary students understand them, we must express the thing in mathematical language, so as to say exactly what we mean. With reference to adaptation, there are one or two points which ecologists have had to study, and of which Professor Cowles makes no special mention, viz., the survival of the fittest and the operation of natural selection in the succession of certain plants. In the survival of the fittest species, for instance—what makes these species the fittest? It is their adaptation to their environment. We may be able to disprove certain specific cases of adaptation that have been passing current and taken for granted for years, but can we get rid of the general idea at all?

PROFESSOR COWLES: These are points which I had to leave out of my paper, on account of my limited time. Personally I distinguish between adaptation in the subjective and in the objective sense. It is quite correct to speak in these plants of survival: I object to the use of language implying that these plants adapt themselves in the subjective sense. The use of the word in the objective sense is all right, but the subjective use of it I object to.

PROFESSOR HARSHBERGER: Some one has said that our ideas never keep pace with the growth of our language, and our language never with our ideas. That has always been found the case in making hard and fast terminology. Where we assign a particular name to a definite idea and purpose, in a short time our ideas change so that our term has to be made more elastic. Now it seems to me that one of the difficulties always being met with is having to adapt our language to our changing ideas. Would

it not be better to have a less hard and fast terminology, to have a few terms that are generally applicable, and then use in a definite way a description, so that a person, in reading the description, will of necessity get from that description the idea which the author wishes to convey, and instead of building up a vast terminology, we shall have a few simple terms of general application, and apply these terms with latitude, so that with the growth of our ideas, beginners or even the person who has been accustomed to the use of the words, will have a chance to adapt the new ideas to the old terminology?

PROFESSOR BOLLEY: If, as Professor Cowles says, plants respond to stimulation, will he grant that these responses may be hereditary, and if they are hereditary—why is it not adaptation?

PROFESSOR COWLES: I would rather not go into this question of heredity. I don't think we know enough about it to ask or answer that. I don't believe it has been proved that there could be such response as is suggested, nor have we disproved it.

PRESENT PROBLEMS OF PHYSIOLOGICAL PLANT ECOLOGY

DR. BURTON E. LIVINGSTON

DESERT BOTANICAL LABORATORY

By physiological ecology is here meant merely the study of the factors which determine the occurrence and behavior of plants growing under uncontrolled conditions. Field physiology would be almost a synonym for the term here used. Pure physiology proceeds, as far as is possible, by controlling conditions. By varying known conditions and measuring the plant responses definite relations are established between stimulus and response. But ecology must perforce proceed without the known conditions, without the synthetically built-up environment of pure physiological research. Here it is necessary to measure and *analyze* natural conditions and to relate these to the behavior of the plants. The problem of measuring the plant phenomena, the determination of the number, size, form, structure, etc., of the plants involved, is essentially the same for both lines of study, but that of measuring environmental conditions is, of course, much more difficult where the latter are uncontrolled.

There is a principle of scientific research, that in an investigation which involves the measurement of a number of causal factors and the relation of these factors to resulting conditions, the various measurements should be of as nearly equal accuracy as possible. Where a number of complex factors are to be dealt with, as in ecology, progress must come, on the one hand, from a refinement of methods of measurement and, on the other, from better interpretations of the data resulting from these measurements. According to the principle just stated, we should ever seek to improve those of our methods which are the

least accurate, not those which are the most easily susceptible of improvement. It is, indeed, often a waste of energy to seek the highest possible accuracy in *all* of a series of measurements where one or more are at best of low accuracy. The accuracy of the resulting summation must be subject roughly to the error of the least accurate of the members.

It is not my purpose to submit any recommendations as to improvement in the general philosophy of ecology, although we must all realize that one of our greatest hindrances at present lies in the careless thinking which fills our literature with wrong or at least misleading imaginings, such as are suggested by the Jonah-like words, *adaptation, use, purpose,* etc. It is to certain lines along which improved methods of measurement seem desirable that I wish to call your attention at the present time. Our methods for dealing with the plant responses, with the *effects* of environment, already possess a general accuracy far surpassing that exhibited by the methods employed in measuring the environmental conditions which act as causes. I am unable to avoid mentioning, however, one phase of plant measurement which has so far received an almost insignificant minimum of attention, both from physiologists and ecologists. I refer to the subterranean portions of the plant. The relations existing between the environmental factors and the development and behavior of underground stems have been studied for some forms by Vöchting, Klebs and others. Roots have usually been studied in water or in air and only in the last few years has their behavior in the natural medium, the soil, been seriously taken up. A number of agriculturists have attacked the problem here suggested, but of course with reference to cultivated plants. Freidenfeld has made, as far as I am aware, the first attempt at a really broad study of the ecology of roots. The work of Dr. Cannon on the root systems of desert plants shows how extremely important subterranean competition may sometimes be. It would seem

that the underground portions of ordinary plants are well worthy of more attention than has heretofore been accorded them.

We turn now to the environmental factors. When it is sought to determine the causes influencing the behavior of plants growing under natural conditions, two very different methods may be resorted to, the observational and the experimental. By the experimental method we try to determine, on the one hand, the kind and amount of vegetation and, on the other, the magnitude of the various physical conditions which make up the environment. From these two series of observations are selected paired concomitant factors or groups of factors, and when the same concomitants appear in a number of such pairs the conclusion is drawn that the relation between the paired factors is a causal one. By the experimental method we seek to control the conditions to a greater or less degree, either synthetizing an artificial environment (experimental physiology), or growing the same plant forms under various natural environmental complexes. This sort of work may be termed experimental ecology. In so far as the environment is artificially synthetized, it is comparatively easy of measurement, but where natural conditions are allowed to obtain, the experimental and the observational methods both require the measurement of uncontrolled factors, and thus present great difficulties.

The complexity of natural conditions makes it necessary often to break them up into component parts and to measure the parts separately. For convenience in handling, these factors have been classified into climatic and edaphic, but I fail to see that such a classification has any relation to the activities of the plant. I shall, therefore, speak here merely of environmental factors, classifying them, for ease in discussion, into those which are active above the soil surface and those which are active below it. Each group must, of course, be further analyzed according to the purposes of the investigation. But it must be remembered that the data from separate com-

ponent factors usually need to be again summed in order to express the environment as a whole. For the great general problems of plant geography it seems inadvisable to attempt too extended an analysis, rather is it better to seek methods of measurement which will furnish integrated evaluations of groups of environmental conditions. With our present lack of knowledge, the pressing of the analysis too far often results in such a complex of data that an interpretation is impossible. A fairly satisfactory integration of the main air factors seems to be furnished by the atmometer; as to the soil factors, we have made hardly a beginning in this direction. In the following paragraphs I shall first consider the measurement of the air factors, denoting by this term all factors which are active above the soil surface, whether or not the air is actually involved.

Atmospheric Factors.—Atmospheric pressure can be easily measured by means of the barometer, curves are automatically constructed by the barograph. Considering the perfection of this instrument, it is rather unfortunate for ecology that the plant is so little influenced by the natural variations in atmospheric pressure.

Temperature is very important in plant activities, and we have practically perfect instruments for its measurement and for the construction of its curve. Unfortunately we have as yet no well-tested method by which temperature can be interpreted in regard to its effect. A beginning which promises much has been made by Dr. MacDougal with his integration of the thermograph record and Professor Lloyd has told me of a new method devised by him for interpreting maxima and minima. Here lies one of the best fields for the scientific ecologist with a mathematical turn of mind.

Wind velocity can be measured and recorded by means of the ordinary forms of anemometer, but the instruments are not well suited to field work, largely on account of their expense. Perhaps improvement may be forthcoming along this line.

The conditions of humidity, which appear to be so important to plant life, can best be measured directly by means of the dew-point apparatus, but the instrument is not as satisfactory in the operation as could be desired. The whirled psychrometer and the wet and dry bulb thermometer are more easily operated and are quite satisfactory as regards results, especially where the humidities dealt with are not too low. Attention may be called here, however, to the inadequacy of the wet and dry bulb thermometer without a strong current of air. The current should be so strong that any increase in its velocity would produce no further lowering of the temperature of the wet bulb. The hair hygrometer is unreliable unless often standardized by some other instrument. Especially is this so in regions where the humidity is usually low or where its fluctuations are very great. Much improvement is surely possible in connection with this factor.

The evaporating power of the air, an integration of the effects of temperature, wind velocity, relative humidity, and, to some extent, of light intensity, is at least not as difficult of measurement as formerly. The porous cup atmometer can be made to give data for a curve as well as a final integration for a long period. It seems that we may expect much from this or some similar instrument.

Precipitation data are easy to obtain with amply sufficient accuracy, but the factors of superficial and subterranean run-off as well as that of evaporation from the soil surface (all of which are almost hopelessly difficult to measure) make these data very hard to interpret, except for particular localities. Their final interpretation will probably go hand in hand with that of evaporation and soil moisture.

For the measurement of light intensity—a factor which has been shown conclusively to be of prime importance in many ecological problems—we have at present no reliable and practical instrument. The delicate bolometer

would doubtless give the data needed, but it is not well suited to field work and is at best too expensive. The so-called photometers (such as those used in photography) are unsatisfactory in the extreme, both theoretically and practically. They are, of course, not photometers at all, but actinometers, and for our purpose it is to be remembered that the shorter light waves are at least not the most important in plant activity. Here again is a field that should prove wonderfully fertile to him who has the courage and patience to cultivate it.

The determination of the composition of the atmosphere is important in certain lines of investigation and in the solution of general ecological problems in certain regions. For this purpose the methods already at hand are perhaps satisfactory enough, though we are unable to obtain automatic records of fluctuations in these conditions.

Soil Factors.—If the factors active above the soil surface present great difficulties, those active in the soil present greater ones. What knowledge has been gained by the agriculturists is seldom at the disposal of the ecologist, perhaps partly from the nature of the agricultural literature, and partly from a too common feeling that agriculture and ecology are far apart. (It appears to me that ecology is the legitimate and necessary meeting-place for scientific botany and scientific and practical agriculture.) But the agriculturists have not made any very great progress in this field. Their measurements of soil conditions are too often merely determinations of the various amounts of inorganic salts which can be extracted from the soil by one or another cleverly chosen solvent. In some cases determinations are made of the total amount of organic matter in the soil, but it appears that these chemical results lack much in ease of interpretation, so much that they are of little value to the ecologist.

Soils have been classified by various workers according to the size of the component particles, but I have not

found any adequate method of interpretation by which the data of the physical analysis may be made to aid in the explanation of vegetational conditions. There is no doubt that these data contain much valuable information, if we but knew how to interpret them.

A beginning has been made in the important and fundamental inquiry into the attraction of the soil for water and the ability of the soil to conduct water to plant roots, but our ignorance in this regard is even more dense than that concerning the normal physiology of the roots themselves.

The geological origin of soils (a subject which makes up a large portion of the text-books on soils) is of no possible importance in either agriculture or ecology. Mitscherlich—the author of the most scientific book on soils which I have come upon—says in his preface,

> For our cultivated plants the geological origin of the soil in which they grow is in no way important; the growth of the plants must always depend upon the *present* physical and chemical constitution of the soil.

Of course this is just as true of uncultivated forms. But attention needs to be called here to the principle already mentioned, namely, that in the pioneer work in such a field as this it is often not well to analyze the great general factors to too great an extent. Great general vegetational features may be compared with great general soil features, and wonderfully enlightening results have come from such comparisons, as, for example, those obtained by Dr. Cowles and his associates in this field.

The possible importance of small amounts of organic chemical substances in the soil has been strongly emphasized by the work of the Bureau of Soils and by that of Dr. Dachnowski and others, and evidence in this regard is rapidly accumulating from all parts of the world. There is now little reason to doubt that bog soils and others which are poorly drained owe the character of their vegetation in great part to the presence in the soil of toxic bodies. There is evidence that many well-

drained soils contain similar substances. The ecologist can not afford to neglect this important line of advance.

The water conditions of the soil have not received the attention which their importance justifies. For determining the amount of soil moisture our methods are confessedly crude and unsatisfactory, yet they have not been employed as extensively as their accuracy seems to justify. Graphs of the fluctuations in the water content have yet to be constructed, although their construction is comparatively simple and their value for our purpose must be very great. Such curves should replace the bare and almost useless data of precipitation and run-off. Improved methods of measuring soil moisture will of course be of great value, if such can be devised.

As to the rate at which the soil can supply water to the plant—quite a different question from that dealing with the amount of soil moisture—we know almost nothing. This rate of possible supply, or the resistance offered by the soil to water absorption by roots, is, I think, perhaps at present the most important problem in all ecology, and it has hardly been touched upon. But the problems here suggested seem to be as difficult as they are important.

We know almost nothing in a quantitative way about the relations between the oxygen of the soil and plant development. If this field should be developed we should undoubtedly be placed in condition to explain many dark and complicated points. The capillary power of the soil apparently determines, other things being equal, both the rate of water supply and that of oxygen supply, and perhaps the best that can be done here, in the absence of more perfect methods, is to study plant behavior with reference to capillary power and water content. But ecologists have hardly even attempted to relate the easily determined capillary power (which is constant in any given soil) to the vegetation, and it is difficult to foresee what important results might be forthcoming from such a simple study.

The temperature of the soil can be measured and recorded with about as great ease as can that of the air. But we meet here the same difficulties in regard to interpretation.

Finally, for a goodly number of ecological investigations, the bacterial flora of the soil must be investigated. The agriculturists have made good progress here and we may do well to follow them. The possibilities are very great.

In conclusion I should like to call attention to what appears to me to be the one great general need of ecological work, namely, the need of quantitative studies. It is only through such studies that the science of the relation of the plant to its environment can make real progress.

Discussion of Dr. Livingston's Paper.

Dr. Burns: I am heartily in accord with all Dr. Livingston has said, and I have a lot of records of light readings, that I think I have had for the past six or seven years, that I don't know what to do with. An ecological work, for instance, will dilate on rain force, and then leave that alone, and presently suggest something entirely different. It seems to me that we could work on something in the line of the determination of the maximum and minimum of light, and along this line I have been trying to work out the amount of shade that these plants can endure before they will die out and be succeeded by some other plant, but I have not got on very far.

Dr. Pond: It would be very valuable if we had some work bearing upon an analysis of a given factor in a given case, and it may be interesting to know that a recent article really attempts it. I refer to the article of Ball's on "Temperature and Growth." Of course, temperature is an external condition. Its effect on growth may be either unseen or apparent in some outward manifestation. This article shows, by a careful analysis, that the temperature factor in the specific case which he was working on, namely, a fungus,—the temperature factor as applied produced a substance which inhibited growth of that fungus and finally stopped its growth.

Professor Barnes: May I take this opportunity to say that I hope very much some of the reforms will be adopted, not only by ecologists, but also by some other members of the botanical fraternity. Mr. Harshberger's quotation that our ideas never keep pace with the growth of our language, and our language never with our ideas, has more truth in it than we imagine. Our ideas have not always kept pace with the growth of our language (laughter). It is greatly to be hoped that the language will not be strained any farther. We need no extensive growth of that, and while far be it from a mere editor to suggest to any ecologist that a page of tabular matter not only costs three times as much to set up, but seems

actually useless and trifling, yet I hope that these suggested reforms will become actualities.

DR. LIVINGSTON: In that very connection it occurs to me that perhaps there is another line of ecological work which goes a step farther in clearing up, that is analysis of conditions. What is found out about physical conditions—then comes the question, how do these conditions come into existence? That is, perhaps, a part of the study of ecology. Very often we have to take the analysis back in order to explain how conditions arise; for instance, this plant grows less because of light, heat and moisture conditions. Now I might enquire how these conditions are brought about? By a tree growing alongside or the absence of vegetation—so we see how ecology leads ever to other fields!

DR. GRIFFITHS: I recall, in connection with the gentleman's statement regarding light and heat, a surprising experience I learned of by talking to a commercial gentleman in Arizona—a commercial man but a scientific one at the same time, a gentleman connected with the solar motor industry, of which you have heard a great deal, and I was surprised at the results of his measurement of light and heat, the measurement of heat particularly. He measured heat, of course, in direct relation to his machine—the reflecting surface of his machine—by a thermometer placed in a black box, with its face to the sun, the box simply being an open one, with the open side to the sun. Much to my surprise he informed me positively than an hour's sunlight on the Atlantic Coast was more efficient than an hour's sunlight on the desert of Arizona. Now, that may be an obvious fact to botanists, but it was not to me at the time. I subsequently thought of the matter, and thought possibly I could see reasons for it, but it had never occurred to me before. The result mentioned is possibly due to the presence of a smaller amount of dust in the atmosphere upon the Atlantic Coast. With a heavier rainfall the atmosphere is clearer. The transmission of heat is more certain and undoubtedly his statement was true. He has demonstrated it with his machine. I presume it is due to the presence of a large amount of foreign material in the atmosphere.

NOTES AND LITERATURE

NOTES ON EVOLUTION

The retirement of Ernst Haeckel from his chair in the University of Jena is a punctuation mark—fortunately not a period—in the long and noble story of "*Haeckelismus in der Zoologie.*" I am aware that the coining of this phrase by Karl Semper and the subsequent use of it by some zoologists and many theologists were not of the nature of compliment to the veteran fighting evolutionist of the Thüringian hills. The phrase was meant to connote reproach, but I prefer to see in it an unavoidable recognition of the great influence and importance of Haeckel's work in the history of biology and evolution. We may decry speculation in zoology and phylogeny in evolution, but without scientific imagination we do not go far forward in any science, and the principles of evolution studied without reference to their practise would leave bionomics far more "philosophical" and much less "biological" than we would have it. Even if Haeckel's speculations and vigorous championship of them had done no more than serve as a stimulus to others to work in order to fight them, they would have had their inestimable importance in evolutionary history. As a matter of fact many of the Haeckelian speculations of the early days are now the accepted and incorporated evolution commonplaces of the present day.

Haeckel gives up lecturing to the Jena students and peering over their shoulders at their dissections to devote himself especially to the building up and care of his new Phyletic Museum. He is now seventy-five years old, and for forty-five years has taught, investigated and written at Jena. Now he gives up part of this work to undertake something else in its stead. A glorious record! And one not uncommon in German scholastic life. Leuckart was lecturing vigorously every day in the week except Sunday up to within two weeks of his death at seventy-six, and the number of active and anything but superannuated professors in German universities beyond the Carnegie fund retiring age is suprisingly large.

The new Phyletic Museum at Jena has been established solely

through Haeckel's personal activity and largely through his personal financial aid. He has given to it 30,000 M. of money and his private library and collections. The building, for which original gifts amounting to 100,000 M. were obtained is now finished and the gathering together and arrangement of collections are going on. It is hoped to have sufficient material on hand and arranged by next spring (1910) to justify the public opening. The building was formally taken over by the University of Jena last July (1908) on the occasion of the celebration of the 350th anniversary of the university's founding. The gathering of the collections and their maintenance must depend entirely in private gifts, and Haeckel makes an earnest appeal to all friends of the development theory for financial aid. Money may be sent to the *Rentamt der Universität Jena, Jenergasse 8, Jena.* Donors of sums of 10,000 M., or over, will have their names engraved on a tablet of "*Ewige Mitglieder des Phyletischen Senates*" placed in the entrance hall of the museum. Professor Haeckel writes in a recent letter that the total expense of establishing the museum will be about 200,000 M., of which 130,000 M. have so far been raised.

. . . . . .

In Germany there goes on a steady discussion of the *Vitalismus versus Mechanismus* subject. There is a constant running disputational conflict between the mechanicalists and the neo-vitalists. The latter find their champion in Hans Driesch, while among the former Otto zur Strassen is one of the most active: If Driesch were not so keen in his criticisms and so adroit in his argumentation victory would have been long ago with his antagonists, for he supports an impossible position. But he uses the method of offense and not of defense; he attacks the weak places in mechanicalism and constantly shifts the burden of proof to the shoulders of the mechanicalists. It is the method made famous, and for long successful, by Weismann, in his war on neo-Lamarckism. But Weismann had in the end, when his position was attacked, to make great concessions, and so it will be with Driesch. Neo-vitalism is really not new, despite its new terminology, but is simply paleo-vitalism very adroitly rehabilitated; and vitalism under any form is irreconcilable with the spirit of scientific progress.

A very interesting example of the advance of mechanicalism at the expense of vitalism on one hand and finalism on the other,

is that of the attitude and work of Dr Pierre Janet, the brilliant Salpetriere student of nervous functions. In a recent book, "Les Nevroses," and more especially in a course of lectures now being given in the Collège de France on the expression and influences of the emotions and sentiments, Janet discards almost entirely the finalistic explanations so well established by Darwin's epoch-making book. In their place he substitutes mechanistic explanations, and his reasoning has great cogency. The finalistic type of explanation of vital phenomena is very plausible and seizing. We snarl when we are angry because we want to scare our neighbor by showing him we are about to bite; or rather, as we no longer bite, we do it because our ancestors did when they wanted to warn their neighbors to keep to their own tree; and we smile because it is useful to show an opposite state of feeling.

But Janet—and others—find that smiling is the mechanically produced contortion of muscular stimulus due to strong emotional shock or mental agitation, and this mental agitation is not at all necessarily one of joy or friendliness or risibility. We smile often when we want to weep, when we are surprised, when we are embarrassed, when we are terrified. The facial muscles are roughly divisible into two unequal sets; one, above, of more and stronger muscles; the other, below, of fewer and weaker ones. When the stimulus comes the muscular pull of the upper set is stronger and our mouth corners go up and the contortion we call a smile is produced. But various emotions may produce the stimulus. If the contortion, that is the smile, is useful, well and good; but it is not a result of usefulness.

A brick is red because it contains by very virtue of being a brick certain chemical components in physical state, of which an attribute is redness. We ask for no further explanation of the brick's color. But let a butterfly's wing be red, and though the waste uric granules in its cuticular scales be of chemical and physical nature to compel them to absorb other colors and reflect red just as brick stuff does, we demand more explaining. We must have utility in this red; we must have a finalistic explanation, and if this explanation be not readily afforded by Darwinian selection or Lamarckian adaptation we have still left the ever-ready and always sufficient explanation of vitalism. The butterfly's wing is usefully red because the butterfly is alive.

We must admire the durability of the good old inheritance of acquired characters problem, even if its repeated resuscitation is sometimes a little less than interesting to us. However, our lessening of interest in it in no way reflects any lessening of its importance. It is still the *crux* of the whole species-forming problem. Neither mutations-theory nor Mendelism make its solution any less imperatively needed.

A recent important contribution, not of discussion alone but of new facts, to the inheritance of acquired characters problem is that of Jennings, who finds that, contrary to the admission on theoretical basis of even some of the most thoroughgoing anti-Lamarckians, acquired characters are not inherited in the Protozoa; at least in those Protozoa which were the subjects of Jennings's brilliant observation and experimentation. This may be a serious blow to the neo-Lamarckian side of the case—or it may not. It is if the old statement of the problem is to be always adhered to, but for some time now this statement has been recognized to be faulty and outworn. The neo-Lamarckian, taking the aggressive, prefers to put it this way: How are we to explain the fact that heritable differences distinguishing species or constant varieties (elementary species?) are often identical with those differences, uninherited, which can be produced ontogenetically among individuals of a single species of the group by submitting them to varying environmental or nutritional conditions? The fact exists and the presumption that it raises is that these identical species (heritable) differences have had the same ultimate causes which under our very eyes produce the non-heritable differences of the ontogenic varieties.

What is needed is the mechanism of cumulation or conversion of the non-heritable differences into identical heritable ones. This mechanism must, of course, concern itself with reproduction, with the germ-cells; and put as Jennings strongly puts it, it seems at first sight as if it must be an impossibly complex mechanism. But after all it is the change that has to be complex. The mechanism needed is one capable of producing changes of seeming great complexity. But comparatively simple mechanical transformers that produce very complex physiological changes are not unknown in biology, and there may, after all, be one awaiting discovery by Jennings, or some other

equally ingenious and persistent student of this good old enduring problem of acquired characters.

V. L. K.

PARIS, March, 1909.

DE VRIES'S SPECIES AND VARIETIES

Species and Varieties.—About two years ago De Vries's "Species and Varieties: their Origin by Mutation" was translated into German. A translation[1] of the same work has now appeared in French and no doubt it will ere long find a place in the literature of a number of other tongues.

As the first book which presented in a popular form the distinction between fluctuations and mutations, the world-wide circulation of this book means much for the advancement of modern biological conceptions. This is particularly true because a just delimitation of these two kinds of variations has been made, and can be made, only through the application of experimental methods. The result of the enlarged circulation of this work must be to stimulate the use of these methods among the biologists of every country in which it is made accessible.

The French edition was translated by Dr. L. Blaringhem, who is already well known because of his numerous studies on variations apparently induced by traumatism. He was a student of the well-known French biologist, the late Professor A. Giard, and to the memory of the latter, the French edition is dedicated. Professor Giard was to have written a preface to this edition, but illness which later resulted in his death rendered this impossible. A very brief prefatory note by the translator and one by the author are the only additions to the text of the English edition.

Already some subjects considered in this book could advangeously receive a somewhat different treatment, but it is perhaps better to allow the book to stand as it was originally written, so to take its position as a classic, retaining a historical value when its current biological value shall have been eclipsed by other works presenting the results of subsequent experimentation. This is evidently the attitude assumed by the author and

[1] De Vries, H. "Espèces et variétés: leur naissance par Mutation," *Traduit de l'Anglais par L. Blaringhem*, pp. viii + 548, 1909. Paris: Felix Alcan.

translator, in presenting this edition without amendment of any kind.

GEORGE H. SHULL.

EMBRYOLOGY

On the Totipotence of the First Two Blastomeres of the Frog's Egg.—It was found by Roux that if one of the first two blastomeres of the frog's egg is injured with a hot needle, the uninjured blastomere will develop into a *half* embryo. Morgan found, however, that if the egg were kept in an inverted position after the injury of one blastomere, the other would develop into a *whole* embryo. He attributes this difference to the rearrangement of the "mosaic" structure of the egg by flowing of substance, of different specific gravity (Born). However, he suggested to me that the half embryo obtained by Roux might be due to the presence of the injured blastomere. In Triton, when the first two blastomeres are separated, each gives rise to a whole embryo (in case the first cleavage plane would have become the median plane). I have been trying various methods for removing one of the first two blastomeres of the frog's egg, and succeeded in getting a small per cent. of the remaining blastomeres (of *Chorophilus triseriatus*) to develop. The puncture of the egg membrane caused it to shrink down on the remaining blastomere and left an opening for bacteria. Although there was a great mortality in the operated eggs, quite a number of them gastrulated (*as wholes*), and several of them reached the tadpole stage. The pressure of the egg membrane seemed to hinder their further development and none of them hatched, although one lived until I fixed it for sectioning, after the control eggs had hatched. In no case was a half gastrula found, and as this is the earliest stage at which the bilateral symmetry is very pronounced, *all of the embryos were wholes as far as could be observed.* Probably all operated eggs in which the median plane would not have coincided with the first cleavage plane died before gastrulation.

J. F. MCCLENDON.

UNIVERSITY OF MISSOURI, April 8, 1909.

The American Naturalist

A Monthly Journal, established in 1867, Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Organic Evolution and Heredity

CONTENTS OF THE DECEMBER NUMBER

Some Physiological Aspects of Radium Rays. Professor C. STUART GAGER.

On the Origin of Structures in Plants. W. A. CANNON.

Origin and Formation of the Froth in Spittle Insects. BRAXTON H. GUILBEAU.

Shorter Articles and Correspondence: Peculiar Abnormal Teeth in a Jack Rabbit. WILLIAM A. HILTON.

Notes and Literature: *Ichthyology*—Ichthyological Notes, President DAVID STARR JORDAN. *The Inheritance of Sex in Higher Plants*—Digest of Professor C. Correns's Memoir: Professor H. E. JORDAN.

Title Page and Index to Volume XLII.

CONTENTS OF THE JANUARY NUMBER

Juvenile Kelps and the Recapitulation Theory. Professor ROBERT F. GRIGGS.

The Larva and Spat of the Canadian Oyster, Dr. J. STAFFORD.

Shorter Articles and Correspondence: Some Notes on the Traditions of the Natives of Northeastern Siberia about the Mammoth, WALDEMAR JOCHELSON. Age of Trotting Horse Sires, F. R. MARSHALL. The Occurrence of *Batrachoceps attenuatus* and *Autodax lugubris* in Southern California, WILLIAM A. HILTON.

Notes and Literature: *Experimental Evolution*—The Effect of the Environment upon Animals, Dr. FRANK E. LUTZ. *Experimental Zoology*—The Influence of the Size of the Egg and Temperature on the Growth of the Frog, SERGIUS MORGULIS. *Parasitology*—Cestodes of Birds, Professor HENRY B. WARD.

CONTENTS OF THE FEBRUARY NUMBER

Charles Darwin and the Mutation Theory. CHARLES F. COX.

Juvenile Kelps and the Recapitulation Theory. II. Professor ROBERT F. GRIGGS.

Notes and Literature: *Plant Phylogeny*—The Origin of the Archegoniates, Dr. BRADLEY M. DAVIS. *Holothurians*—Clark's The Apodous Holothurians, W. K. FISHER. *Lepidoptera*—The Blue Butterflies of the Genus Celastrina, Professor T. D. A. COCKERELL. *Vertebrate Paleontology*—The Lysorophidæ; Stegocephala; The Cotylosauria; The Oldest Known Reptile; The Age of the Gaskohle; Bison Occidentalis; Nectosaurus; Callibrachion, Dr. ROY L. MOODIE. *Parasitology*—The Sleeping Sickness Bureau, Professor HENRY B. WARD. *Exploration*—Camp-fires on Desert and Lava, Dr. ROY L. MOODIE.

CONTENTS OF MARCH NUMBER

Invitation Papers at the Baltimore Meeting of the Botanical Society of America; Darwin Memorial Session:—
Darwin as a Naturalist; Darwin's Work on Cross Pollination in Plants. Professor WILLIAM TRELEASE.
Darwin's Influence upon Plant Geography and Ecology. Professor FREDERIC E. CLEMENTS.
Darwin's Work on Movement in Plants. Professor HERBERT MAULE RICHARDS.

An Examination of Darwin's "Origin of Species" in the Light of Recent Observations and Experiments. Professor EDWIN LINTON.

The Distinction between Development and Heredity in Inbreeding. Dr. EDWARD M. EAST.

Breeding Experiments with Rats. Professor T. H. MORGAN.

Shorter Articles and Discussion: The Chub and the Texas Horn Fly, Dr. ROY L. MOODIE. A New Camel from the Lower Miocene of Nebraska, HAROLD JAMES COOK.

Notes and Literature: *Heredity*—The Chondriosomes as Bearers of the Hereditary Qualities, F. PAYNE. Cultural Bed Mutations in the Potato.

CONTENTS OF THE APRIL NUMBER

Heredity of Hair Color in Man. GERTRUDE C. DAVENPORT and CHARLES C. DAVENPORT.

A Mechanism for Organic Correlation. Professor G. H. PARKER.

Recent Advances in the Study of Vascular Anatomy.
Vascular Anatomy and the Reproductive Structures. Professor JOHN M. COULTER.
The Progress of Plant Anatomy During the Last Decade. Professor EDWARD C. JEFFREY.

Shorter Articles and Correspondence: A Note on the Degree of Accuracy of the Biometric Constants, DR. RAYMOND PEARL. Pure Strains as Artifacts of Breeding. O. F. COOK.

Notes and Literature: *Heredity*—The Nature of "Unit" Characters, DR. W. J. SPILLMAN. *Environment*—DR. FRANK E. LUTZ. *Experimental Zoology*—Hybridology and Gynandromorphism, Professor T. H MORGAN. *Echinodermata*—Red Sea Crinoids, DR. AUSTIN HOBART CLARK.

CONTENTS OF THE MAY NUMBER

The Categories of Variation. Professor S. J. HOLMES.

The General Entomological Ecology of the Indian Corn Plant. S. A. FORBES.

Notes and Literature: *Biometrics*—Some Recent Studies on Growth. DR. RAYMOND PEARL. *Experimental Zoology*—Cuénot on the Honey Bee, Professor T. H. MORGAN. *The Upholding of Darwin*—Poulton and Plate on Evolution, V. L. K.

Single Number 35 Cents **Yearly Subscription, $4.00**

The NATURALIST will be sent to new subscribers for four months for One Dollar

THE SCIENCE PRESS

Garrison, N. Y. **Sub-Station 84: NEW YORK** **Lancaster, Pa.**

SEX AND SOCIETY

BY

WILLIAM I. THOMAS

THIS volume approaches the question of woman and her position in society from a new standpoint. It recognizes that sex is a fundamental factor in the origin and development of social institutions and occupational activities, and that a number of social forms and forces are of sexual origin.

After a preliminary paper in which the organic differences of the two sexes are analyzed, there follows a series of studies on the relation of sex to social feeling and stimulation, and the influence of sex in securing a system of social control; the psychology of the maternal system of tribal organization; sex as a factor in the differentiation of occupations in early society, and the relation of woman to early industry and invention; the relation of sex to the origin of morality; the origin of exogamy; the origin and psychology of modesty and clothing.

In the last two papers, on "The Adventitious Character of Woman" and "The Mind of Woman and the Lower Races," modern woman is interpreted from the standpoint of certain conventions and prejudices which emanate from the fact of sex, and which have excluded her from full participation in the activities of the "white man's world," with the result that she develops a type of mind and character not representative of the natural traits of her sex.

Former treatises on the "woman question" have dealt in the main in a descriptive way with the history of marriage, or at least only with the details of the development of the marriage system, and have failed to present a theory which makes clear the *significance* of the present position of woman in society. The volume by Professor Thomas is the first attempt made to estimate the influence of the fact of sex on the origin and development of human society.

300 pages, 12mo, cloth; net $1.50, postpaid $1.65

Address Dept. 62

THE UNIVERSITY OF CHICAGO PRESS

CHICAGO NEW YORK

VOL. XLIII, NO. 511 JULY, 1909

THE AMERICAN NATURALIST

A MONTHLY JOURNAL
Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

CONTENTS

		Page
I.	Selection Index Numbers and their Use in Breeding. Dr. RAYMOND PEARL and FRANK M. SURFACE	385
II.	A Contribution to the Theory of Orthogenesis. Dr. ALEXANDER G. RUTHVEN	401
III.	The "Presence and Absence" Hypothesis. Dr. GEORGE HARRISON SHULL	410
IV.	Present Problems in Plant Ecology: Vegetation and Altitude. Professor CHARLES H. SHAW	420
V.	Shorter Articles and Correspondence: Pleistocene Swamp Deposits in Virginia. Dr. EDWARD W. BERRY	432
VI.	Notes and Literature: *Heredity*—A Case of Non-Mendelian Heredity. DR. W. J. SPILLMAN	437

THE SCIENCE PRESS

LANCASTER, PA. GARRISON, N. Y.

NEW YORK: SUB-STATION 84

The American Naturalist

MSS. intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS

Lancaster, Pa. Garrison, N. Y.

NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

Important New Scientific Books

PUBLISHED BY THE MACMILLAN COMPANY

Botany

The Origin of a Land Flora. A Theory based upon the facts of Alternation. By F. O. BOWER, Sc.D., F.R.S. With numerous illustrations.

Cloth, gilt top, xi+727 pp., illus., index, 8vo, $5.50 net.

NOTE.—A profound study in the morphology of the lowest forms of plants, with special reference to the development of their reproductive systems. The author endeavors to show that the present land flora has originated from an aquatic ancestor, and traces the methods of specialization to the land habit, and the establishment of the forms of the higher plants. A book of the highest importance not only to botanists but to biologists in general.

NEW AND STANDARD HAND-BOOKS ON AGRICULTURE, ETC.

Elements of Agriculture, Southern and Western. By W. C. WELBORN, B.S., M.S., M.P.A.

Cloth, xvi+329 pp., illus., appendix, glossary, index, 12mo, $.75 net.

NOTE.—This is a thoroughly modern treatise on farming as practiced in the Gulf States, from the point of view of the scientific agriculturist. It is adapted to school use, but is of practical service to any farmer in that part of the country. The author is vice-director of the Texas Experiment Station.

Re-issues of the highly valued Hand-Books known as the Garden Craft and Rural Science Series, edited by L. H. BAILEY, of Cornell University, Editor of "Cyclopedia of American Horticulture," "Cyclopedia of American Agriculture," etc.

The Principles of Fruit Growing. By L. H. BAILEY.
Tenth Edition, $1.50 net, by mail $1.66.

Irrigation and Drainage. By F. H. KING.
Fifth Edition, $1.50 net, by mail $1.68.

Principles of Vegetable Gardening. By L. H. BAILEY.
Sixth Edition, $1.50 net, by mail $1.68.

Bush Fruits. By FRED W. CARD.
Fourth Edition, $1.50 net, by mail $1.66.

Fertilizers. By EDWARD B. VOORHEES.
Tenth Edition, $1.25 net, by mail $1.38

Farm Poultry. By GEO. C. WATSON.
Sixth Edition, $1.25 net, by mail $1.42

Published By **The Macmillan Company** 64-66 5th Ave., New York

THE
AMERICAN NATURALIST

VOL. XLIII *July, 1909* No. 511

SELECTION INDEX NUMBERS AND THEIR USE IN BREEDING [1]

DR. RAYMOND PEARL AND FRANK M. SURFACE
AGRICULTURAL EXPERIMENT STATION, UNIVERSITY OF MAINE

I. THE NATURE OF THE SELECTION PROCESS

WHATEVER one's views regarding the relative importance of different theories as to the method of inheritance for practical breeding, it must be recognized that the vast majority of all the actual breeding operations which are being carried on by plant and animal breeders at the present time are conducted by some method of selection. The belief is firmly held by most practical breeders that the bulk of the improvement which has been made in domestic plants and animals has been as the result of selection. While it is also coming to be recognized that hybridization may play an extremely important part in breeding operations either by causing increased variation or by bringing about a recombination of characters, according to Mendelian principles, yet selection must always be used as a supplement to hybridizing in practical breeding. The higher degrees of perfection demanded in judging ring and show room are only attained by the most careful and close selection. The manner in which successful selection operates, that is whether by isolation of pure or homozygote strains from a mixed population or by the gradual cumulative effect of adding together slight

[1] Papers from the Biological Laboratory of the Maine Agricultural Experiment Station, Orono, Maine. No. 11.

fluctuating variations, need not here concern us. In either case the breeder is continually meeting the same practical problem of selecting breeding stock with reference to several characters.

It is an obvious fact that a breeder practically never wishes to improve only one single characteristic of the plant or animal which he is breeding. What is usually desired is to improve several characteristics at the same time. Thus, with dairy cattle, while the main object in breeding is to increase the amount and quality of the milk other things such as constitutional vigor, breeding capacity and the like can not be lost sight of in making the selections of breeding stock. Or in maize breeding, to take an illustration from the plant side, while one may be desirous of increasing the protein content of maize, in breeding for it he must always keep in mind the conformation of the ear, size of ear, yield and a whole series of other characteristics.

While it is generally true that one wishes in practical breeding to improve more than one feature at the same time, it is an extremely difficult thing to make concurrently close selection of two or more characteristics of an organism. This difficulty is essentially a psychological one. It is the difficulty of trying to do more than one thing with the mind at the same time. The way in which this operates in breeding by the method of selection may be illustrated by an example. Suppose one is attempting to improve a strain of maize with respect to (*a*) earliness and to (*b*) conformation of the ear at the same time. When beginning his field selection of plants he makes a resolution that he will keep to a certain standard with reference to both of these characteristics and will accept nothing below those standards. Presently he comes to a plant which is by far the earliest in the field. It by a great deal surpasses all others in respect to this character, yet unfortunately the ear of this plant falls below his chosen standard for conformation of ear. What is to be done? Logically the plant ought to be rejected. But

if the breeder is deeply interested in improving the corn with respect to earliness what actually will happen will be this: he will decide to take this plant on account of its earliness and in spite of the defects of the ear. In selection work every degree of compromise of this kind is made and the larger the number of characters one attempts to deal with at the same time the more compromises are made. Where shall the line be drawn beyond which further compromise shall not be permissible?

II. The Theory of Selection Index Numbers

It would seem to be highly desirable to devise, if possible, some method for the use of the breeder who is practising selection which would get over in a greater or less degree the difficulty which has been outlined in the preceding section. What is needed is some method whereby a selection of several characters may be made at the same time in an absolutely impersonal and impartial manner without throwing out absolutely those individuals which are especially good with respect to a single one of the group of characters undergoing selection and mediocre or poor with respect to the other characters of the group. It has occurred to us that a way of reaching this desired end is found in the use of what we have called "selection index numbers," borrowing the terminology and something of the idea from the literature of political economy.

An "index number" in the sense here used means a single mathematical function which combines in itself the values of several independent or correlated variables. In such a function each of the variables may be weighted in any desired manner to meet the needs of the particular problem. Having decided the relative degree to which each variable shall be weighted, the index number as finally calculated gives an absolutely impartial and impersonal summing up of the total combined value or effect of the variables entering into it.

The theory of a breeding index number may be illus-

trated by a concrete example. Let the matter of improving maize by selective breeding be taken. Suppose that a breeder starts with a promising variety of yellow dent corn. This variety, while promising, has never been improved by breeding at all. The ears are only fair in respect to size and shape. The principal aim of the breeder of this corn, let us suppose, is to increase the "earliness" (*i. e.*, shorten the time of maturing), but at the same time he wishes to improve the other characteristics of the corn—size and shape of ear, relative proportion of corn on cob, and yield per acre. In making field selections of plants to furnish seed for testing out by the "ear-row" or other method, the breeder will endeavor to select with reference to as many as possible of the points enumerated above in addition to "earliness." Further it will be desired after the ears have been harvested and dried to take careful account in selecting the seed of at least the following points: Shape of ear, length of ear, circumference of ear, condition of tip and butt of the ear, kernel shape, germination and proportion of shelled corn to cob. Now if a plant happens to be especially early, even though it be relatively poor in respect to these ear characters, it is likely to be selected to furnish seed, in spite of these defects. But it is possible to devise a formula for a selection index number which shall give whatever weight may be previously agreed upon to each of these several variable characters of the corn which have been enumerated. Having settled upon a particular formula, the selection of seed then becomes essentially a purely mechanical matter so far as the characters included in the formula are concerned. The value of the index will be determined by the relative contributions from each of the included variables. If the breeder calculates such a selection index number, and takes no ears with an index below that standard, it will then be possible for him to select with reference to a series of characters in an unbiased and impartial manner.

Analytically considered a selection index is an expression of the general form

$$I_1 = \phi(x, y, p, q, \cdots, w) \qquad (1)$$

where I_1 denotes the selection index and x, y, p, q, etc., are the variables upon which it desired to carry out selection. The practical question which has to be solved in forming a selection index in any given case as to what shall be the form of the function ϕ. The formula for an index should fulfill the following requirements:

1. It should be simple and easily calculated.

2. The value of the index should increase as the desirability of the individual as a breeder increases.

3. The index should be relatively more sensitive to small changes in important characters than to those in unimportant characters; that is, the variables should be differentially weighted.

4. The value of the index should decrease as undesirable characters become relatively marked.

It has seemed to the writers that to a first approximation the following general form of expression will be found to be well suited for a selection index:

$$I_1 = \frac{ax \pm by \pm cz \pm \cdots \pm nw}{a'p \pm b'q \pm c'r \pm \cdots \pm n't} \qquad (2)$$

In this expression x, y, z, $\cdots$, w are variables which become more desirable (*i. e.*, from the breeder's standpoint) as their values *increase;* whereas p, q, r, $\cdots$, t are variables which become more desirable as their values *decrease.*[2] The quantities a, b, c, $\cdots$, n, and a', b', c' $\cdots$, n' are constants to be given arbitrary values in the proportions that the different variables are to be weighted.

It will be seen that a selection index number as described above is in a sense an adjunct or supplement to a score card. The index affords a means of condensing the entire information which the score card gives into one unit which can be then dealt with individually.

[2] Cf. actual indices for poultry and corn, pp. 392 and 397 *infra.*

Selection indices of the character above described may be separated into two general categories. These categories may for the sake of convenience be designated as (*a*) fundamental and (*b*) special. A selection index is to be regarded as fundamental when it includes in its formula those characters of an organism which every breeder will wish to maintain at a high grade or improve, whatever may be the special purpose for which he is breeding. Thus, for example, in maize breeding whether the breeder is working for high protein or high oil content or earliness, he will always desire to have well-shaped ears with good tips and of good size, a high yield of shelled corn to the acre and good vitality (*i. e.*, germinative capacity) in his seed.

These and other characteristics which we need not take space here to enumerate are in a sense fundamental or universal characteristics which every breeder wishes to improve or, at least, to keep at a high standard. Similar considerations obtain in breeding dairy cattle or poultry for performance. Besides the performance in respect to milk production or egg production every breeder of these animals desires that what may be called the "breeding capacity" of his stock shall be constantly improved or, at least, not impaired. By "breeding capacity" is meant ability to produce numerous and vigorous healthy offspring, to put the matter in the broadest way. An index number which has to do with these universally desired characters may be called the fundamental selection index for each type of organism.

On the other hand, by a special selection index is to be understood one which includes those characteristics which a breeder is specially and particularly working to improve. In the case of the corn breeder working for high protein, the protein content of the ear will constitute one of his special selection indices either by itself or in combination with some other characters. In dairy cow breeding the butter fat content of the milk will be a special selection index.

What may be called the final selection index may be formed by combining mathematically the fundamental and special indices in a single index number.

III. A Selection Index for Poultry

The writers are engaged in the experimental breeding of poultry and of maize with reference to utility characters. One of the special aims of the poultry breeding work is to learn how to fix superior egg production in a strain by breeding. In the corn breeding the chief special aim is to improve a strain of sweet corn in respect to earliness, so that it may mature seed under Maine climatic conditions. In connection with this work the idea of selection index numbers has been developed. It is proposed to discuss here the particular selection indices which we are using for poultry and for sweet corn simply as an illustration of the theory of such index numbers and of their application in actual practical breeding operations. It is not our intention to maintain in the least that the indices here given are the best which could be devised or even that they are not subject to change in our own hands with further experience. They are still in the experimental stage. Our only reason for calling attention to the particular forms of indices which we are using at this time is that we believe that the general idea of selection indices as set forth in this paper may prove to be a useful one to the breeder working in other fields. The fundamental idea of a selection index number is a most elastic one. Any one may adopt and modify these indices and weight the different variables, in any way to suit his individual needs. But there is no doubt that a general plan of this kind becomes more intelligible if concrete illustrations of its operation are given. The specific selection indices now to be discussed are presented solely as illustrations of the general theory.

In the case of poultry breeding a fundamentally desirable thing, whatever may be the special object of the

breeder, is reproductive or breeding capacity in the birds. A "200-egg" hen is of very little value *as a breeder* if she is not able to produce when mated with a good male bird a fair precentage of chickens which will live.

It is very generally stated by practical poultrymen that the point on which it is most often decided whether a given commercial venture in the poultry business shall succeed or fail is the expense involved in the hatching and rearing of the chickens. The female that will produce eggs which will yield a high proportion of chickens from the eggs set, and whose chickens live through to marketable age is an extremely desirable bird from a practical standpoint.

The fundamental selection index which we have chosen for poultry relates primarily to the breeding capacity of the female. The value of this index for a particular bird can only be determined after her breeding capacity has been tested. This poultry selection index comes into application in deciding which of the pullets that have been tested as breeders in their pullet year shall be kept over to be used as breeders in their second year of life.

The formula which has been provisionally adopted in our work as a fundamental poultry selection index is as follows:

$$I_1 = \frac{5(a+b)}{c+d+1}$$

The following scheme shows the meaning of the letters in the formula:

I_1 = general or fundamental poultry selection index for an individual bird.

a = percentage of this bird's eggs which hatched.

b = percentage of eggs actually laid by this bird to the total number it was possible for her to lay between February 1 and June 1 (*i. e.*, the breeding season) of the year for which the index is calculated.

c = percentage of this bird's eggs which were infertile.

d = percentage of chicks hatched from this bird's eggs

which died within three weeks from the date of hatching.

A brief discussion will make clear the reasons why these particular variables are chosen for the index and are arranged in the formula in the manner that they are. A bird's value as a breeder increases as the percentage of her fertile eggs which hatch increases. Therefore *a* should go into the numerator of the index fraction. Similarly a bird's value increases as a breeder in proportion to her egg production in the breeding season. A bird which produces few eggs during the breeding season (whatever she may have done before) *ipso facto* can not produce many chickens. Instead of using the actual egg production in the index the relative or percentage production is used, for reasons which have been discussed in a previous publication by the present writers.[3]

Now in distinction to the factors so far discussed it is clear that a hen's value as a breeder decreases as the number of infertile eggs which she produces in a given time increases. To put this factor into the breeding index is, of course, equivalent to asserting that the hen plays at least an equal part with the cock in determining fertility. This is undoubtedly the case, though it is not the place here to present detailed evidence on the point. Since relatively poor fertility of the eggs is an undesirable characteristic *c* is put in the denominator of the index fraction. The case is the same in regard to *d*. If the chicks produced by a particular bird are weak and die early when given the same treatment as that under which other chicks thrive, it is an indication that that particular bird is not desirable as a breeder.

In order to give a concrete idea of the values which this poultry selection index may take in actual cases Table I has been prepared. This table gives the value of I_1 for a number of pullets which were tested as breeders in the spring of 1908, as well as the values of the component factors in each case. The cases given in the table

[3] Cf. Me. Agric. Expt. Station, Bulletin No. 165, pp. 46–48.

are not a random sample of the breeding flock but were definitely selected to illustrate the behavior of the index.

TABLE I

SHOWING REPRESENTATIVE VALUES OF THE SELECTION INDEX IN POULTRY AND ITS COMPONENT PARTS

DATA FOR BARRED PLYMOUTH ROCK PULLETS[4]

Band No. of Bird.	A Per Cent. of Fertile Eggs Hatched.	B Percentage Breeding Egg Production.	C Percentage of Eggs Infertile.	D Per Cent. of Chicks Dying within 3 Weeks.	Selection Index I_1.	Band No. of Bird.	A Per Cent. of Fertile Eggs Hatched.	B Percentage Breeding Egg Production.	C Percentage of Eggs Infertile.	D Per Cent. of Chicks Dying Within 3 Weeks	Selection Index I_1.
10	21	18.33	36	33.33	2.8	29	28	28.33	27	0	10.0
160	9	15.83	42	0	2.9	23	39	35.83	28	8.33	10.0
402	14	33.33	30	50.00	2.9	428	46	40.08	20	22.22	10.0
352	12	41.67	14	60.00	3.6	122	49	34.17	15	23.53	10.5
358	50	31.67	32	69.23	4.0	375	41	37.50	36	0	10.6
438	35	35.00	45	37.50	4.2	712	42	50.00	20	20.00	11.2
441	38	20.00	33	33.33	4.3	408	48	45.86	16	22.73	11.8
21	25	35.00	14	44.44	5.0	38	61	37.50	9	28.00	13.0
393	12	47.50	9	50.00	5.0	731	27	35.83	23	0	13.1
705	38	26.67	34	25.00	5.4	395	29	37.50	24	0	13.3
717	24	21.67	19	20.00	5.7	443	56	54.17	6	35.29	13.3
39	23	29.17	26	16.67	6.0	409	37	46.67	4	25.00	13.9
377	32	37.50	16	33.33	6.9	771	43	60.00	13	22.22	14.2
746	59	28.33	15	47.06	6.9	19	68	24.17	24	6.66	14.5
87	36	39.17	17	35.71	7.0	152	26	39.17	11	9.09	15.5
359	61	32.50	15	50.00	7.1	366	52	25.83	13	7.14	18.4
442	41	68.33	38	28.57	8.2	768	74	45.00	20	9.38	19.6
400	44	47.50	16	38.10	8.2	434	72	58.33	17	14.28	20.2
27	18	40.00	8.3	25.00	8.5	750	57	52.50	16	10.00	20.3
757	23	51.67	10	30.77	8.9	770	71	50.83	9.8	12.82	25.8
725	33	29.17	6	27.27	9.1	752	48	59.17	6	12.50	27.5
112	17	46.67	18	25.00	9.3	397	38	40.00	6	5.89	30.3
753	61	47.50	46	10.53	9.4	168	88	35.83	4.7	13.89	31.6
407	41	41.67	18	23 53	9.7	749	57	46.50	4	6.45	45.2

From this table the following points are to be noted:

1. The selection index ranges in value between 2.8 and 45.2 in the cases chosen for illustration. These figures do not represent the extreme values which may be obtained for this index. They suffice, however, to bring out the point of practical importance that the index fluctuates through a wide numerical range as the value of the birds as breeders changes.

[4] It should be said that all the records given in this table were made under uniform conditions as to housing, feed, age of birds, etc. The hatching was all done in incubators.

2. A study of the detailed figures of the table makes it apparent that the index is a perfectly impartial and accurate measure of a bird's breeding performance. Thus to take an example, bird no. 402 has a low selection index (2.9), while bird no. 168 has an index more than ten times larger (31.6). Do these figures represent fairly the difference between these two birds in respect to breeding performance? Let us examine the detailed figures. But 14 per cent. of the fertile eggs from bird no. 402 hatched as against 88 per cent. of the fertile eggs of no. 168. In regard to number of eggs laid during the breeding season the two birds are about equal, with what advantage there is in favor of no. 168. But on turning to the question of fertility of eggs we see that 30 per cent. of the eggs of no. 402 were infertile as against only 4.7 per cent. in the case of no. 168. The same condition obtains in regard to the vitality of the chicks. Fifty per cent. of the chicks from no. 402 died before attaining the age of three weeks, whereas but 13.89 per cent. of no. 168's chicks died within this time. There is no doubt of the great superiority of 168 over 402 in breeding performance. The index gives an exact measure of its degree or amount.

3. The detailed figures bring out clearly the further point that the value taken by the index is not unduly influenced by any one factor. Low values for one variable may be offset by high ones in another. In general, the variables which form the numerator of the index fraction are seen to increase as the index increases. The reverse holds in general for the variables in the denominator of the index. The facts regarding the two variables, a (percentage of fertile eggs hatched) and c (percentage of infertile eggs) are shown graphically in Fig. 1.

The diagram shows that the percentage of fertile eggs hatched in general increases as the selection index increases in value, but with much greater fluctuations from bird to bird. On the other hand the percentage of infertile eggs in general decreases as the value of the index increases, but again with much greater fluctuations. The

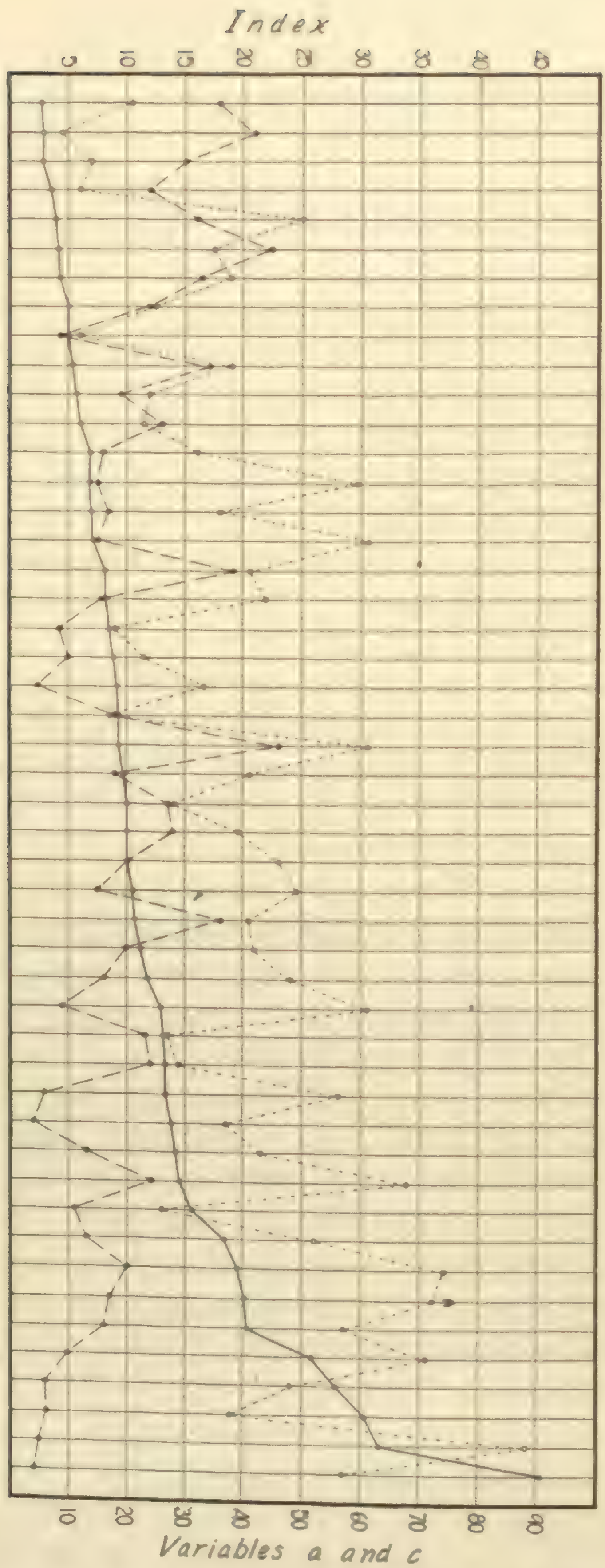


FIG. 1. Diagram showing the relation to the value of the selection index of the order given in Table I; O———O selection index; o.....o percentage of two of the variables entering into it. The abscissæ denote the birds arranged in fertile eggs hatched; ●---● percentage of infertile eggs.

smoothing effect of combining the four variables into one index number appears most clearly from the diagram.

4. In Table I, one half of the birds have a selection index equal to or greater than 10. This is about the value which it would seem desirable to take as a division point in selecting breeders. A bird with an index below 10 can not be regarded as a good breeder.

Summarizing, we believe the poultry selection index described, or some modification of it to suit particular needs, to be a useful aid in practical breeding operations with poultry. It measures in an exact and impartial manner the performance of a bird as a breeder in any given season. On the basis of the knowledge so gained the breeder can select birds which are to be retained for further breeding. It substitutes an exact and impartial measure, in the place of a rough, general impression of the relative effect of several variables.

IV. A Selection Index for Sweet Corn

The idea of selection index numbers is being applied in connection with investigations in breeding sweet corn (*Zea Mays saccharata*). In this work the selection index is based on the characters of the ear. A brief discussion of this index is introduced here for two reasons, viz., (*a*) to illustrate the adaptability of the selection index idea to widely different classes of breeding problems, and (*b*) to show how such index numbers supplement the score card in breeding operations. In planning this corn selection index the underlying idea was that set forth by way of example earlier in the paper (p. 386, *supra*).

The actual index number used for sweet corn has the following formula:

$$I_1 = \frac{A + 3B + 2C}{D + E + F^2}$$

The meaning of the letters in the equation are shown in the following scheme.

A = Length of ear multiplied by the circumference of the ear ($L \times$ Cir.). This gives a measure of the absolute size of the ear.

$$B = \frac{\text{100 times the weight of grains shelled from butt and tip of ear.}}{\text{Total weight of shelled corn from whole ear}}$$

B is the percentage which the grain on butt and tip is of total grain on the ear. This gives a measure of the extent to which ends of the ear are covered with grain.

$$C = \frac{\text{100 times the circumference of the cob at the middle of the ear.}}{\text{Circumference of ear at middle.}}$$

This measures in effect the average percentage depth of kernel (by difference).

$$D = \frac{\text{100 times the weight of the cob.}}{\text{Total weight of shelled corn from the whole ear.}}$$

$E =$ (circumference of ear at butt) $-$ (circumference of ear at tip). A measure of the shape of the ear.

$F =$ 100 $-$ the observed percentage germination of grain from this ear.

All measurements and determinations are made on the thoroughly dried ear and are recorded in centimeters and grams.

As an illustration of the way in which this index is calculated a single example may be worked out in detail.

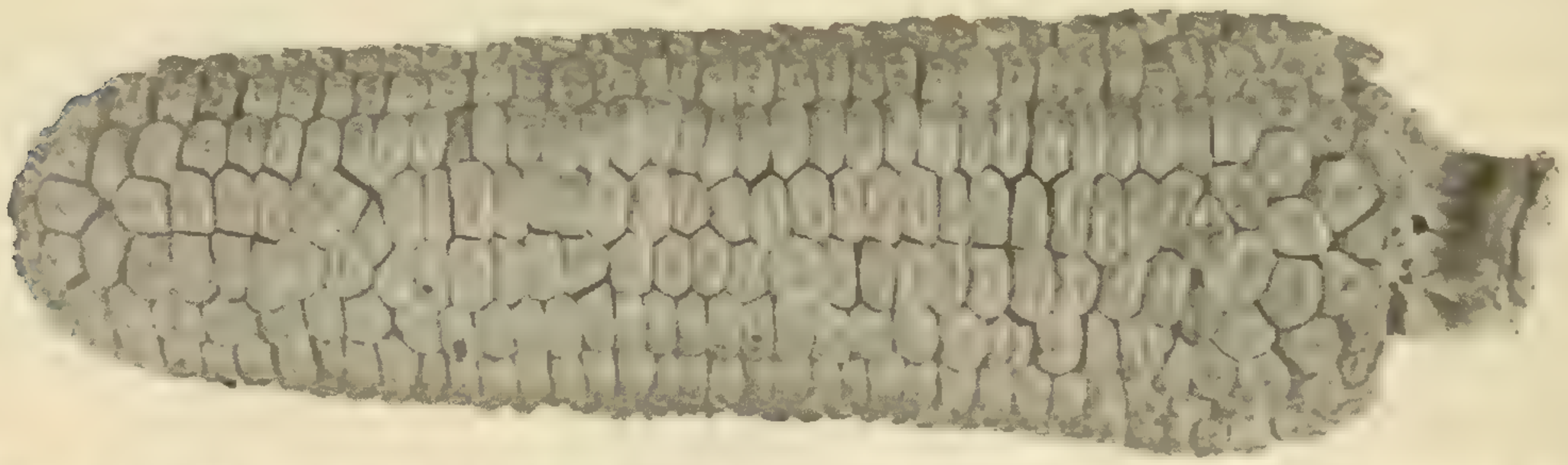


FIG. 2. Photograph of sweet corn ear No. 596 for which the selection index number is calculated in the text.

Let us determine the value of I_1 for the ear of sweet corn shown in Fig. 2, and recorded in our notes as ear No. 596.

For this ear the following measurements were recorded:

Length	14.8 cm.
Circumference	12.9 "
Weight	118.0 gr.
Weight of shelled corn	97.0 "
Weight of corn shelled from butt and tip	22.8 "
Weight of cob	21.0 "
Cob circumference	7.9 cm.
Butt circumference	9.3 "
Tip circumference	6.5 "
Rows	16
Number of kernels in average row	33
Germination (100 kernels tested)	100 per cent.

Using these data to calculate the selection index it appears that:

$$A = 14.8 \times 12.9 = 190.9$$

$$B = \frac{100 \times 22.8}{97.0} = 23.5$$

$$3B = 70.5$$

$$C = \frac{100 \times 7.9}{12.9} = 61.2$$

$$2C = 122.4$$

$$D = \frac{100 \times 21.0}{97.0} = 21.6$$

$$E = 9.3 - 6.5 = 2.8$$

$$F = 100 - 100 = 0$$

$$F^2 = 0$$

Whence we have:

$$I_1 = \frac{190.0 + 70.5 + 122.4}{21.6 + 2.8 + 0} = \frac{333.8}{24.4} = 15.7$$

The value of the index in this case is much above the average for the particular variety of sweet corn of which this ear is a representative. This is, of course, as it should be, since the ear is a particularly fine one for sweet corn. Its aristocratic lineage is apparent from the photograph. Some ears of this variety give a value for the index of as low as 1.0 or even lower. It is obvious that the index number for an ear of one variety is not directly comparable with that for an ear from another

variety. Corn index numbers, as formulated above, are only directly comparable within a single variety. They may of course just as well be used in judging a dent corn, for example, as for the sweet corn here discussed. The average ear of dent corn will obviously give a different value for the index from that given by the average ear of sweet corn.

Any one familiar with the score cards used in judging corn in the various agricultural shows and fairs in this country will recognize that the corn selection index formula here given combines in one expression quantitative determinations of a majority of the characters which appear on the score card. The index in a way takes the place of the judge. It impartially "cuts for each defect" according to a previously agreed upon system of weights. By the combined use of the index number, scales and measuring tape, unconscious or conscious partiality and bias is inevitably and absolutely taken out of the judging. The selection index idea seems capable, when properly developed to meet the needs of particular cases, of supplying in some measure that thing which has been so long desired in all kinds of stock judging, whether of plants or animals, viz., an *absolute* base or datum plane.

V. SUMMARY

The purpose of this paper is to call the attention of those interested in breeding operations to the usefulness of what we have called "selection index numbers" in such work. The idea of such index numbers is to combine in a single numerical expression the values of a series of variable characters with regard to all of which the breeder wishes to practise selection at the same time. The analytical expression of this idea is discussed and its adaptability and usefulness are illustrated by examples drawn from poultry and maize breeding. It is shown that selection index numbers form a valuable adjunct to the score card in stock judging.

A CONTRIBUTION TO THE THEORY OF ORTHOGENESIS [1]

DR. ALEXANDER G. RUTHVEN

UNIVERSITY OF MICHIGAN MUSEUM

SEVERAL reasons have been given why biological discussion has, for a number of years, ceased to center about the fact of evolution and is now chiefly concerned with the factors, for such is evidently the case: the principal aim of modern biological researches is apparently to throw light upon the question of method. It is now a part of common knowledge that Darwin considered the natural selection of fluctuating variations to be the principal factor in evolution, and some of his successors have gone so far as to see in it a sufficient one; but, while few biologists will probably be disposed to deny that natural selection is an efficient factor in evolution, there seems to be now on hand a sufficient body of data to show that it is far from being the only one. Among other methods[2] that have been emphasized, mutation and orthogenesis may be mentioned, each of which has its adherents, and it is the last named of these that seems to be the principal one concerned in the evolution of a group of snakes that I have recently monographed—the genus *Thamnophis* (the garter-snakes).[3]

I will briefly summarize the conditions that prevail in this group:

1. The genus *Thamnophis* consists of four groups of

[1] Read at the Darwinian Celebration of the Michigan Academy of Science, April 1, 1909.

[2] I mention only these three (selection, mutation and orthogenesis), as they appear to me to be the only ones that can be considered to have been dominant methods in the evolution of the forms in the genus that constitutes the basis of this discussion.

[3] Ruthven, Alexander G., "Variations and Genetic Relationships of the Garter-snakes," Bull. 61, U. S. Nat. Museum.

closely related forms, each group ranging both northward and southward from the Mexican plateau (which is their center of dispersal) into North and Middle America.

2. Each group consists of a series of forms, the ranges of which adjoin and correspond to different geographical regions.

3. The forms of the same group may intergrade or not, but in either case they come in contact where the geographic conditions with which they are associated meet, and the areas of transition in characters correspond to the areas of intermediate environmental conditions. When the forms intergrade the transition in characters takes place gradually in the intermediate region, and where there is apparently no intergrading at present the two forms become most like each other in this region, there being no abrupt changes in characters between two directly related forms.

4. Each group tends to become progressively more dwarfed away from the Mexican plateau, each form usually being more dwarfed than its neighbor toward the center of origin, and less so than the representative whose range adjoins it on the side away from the center.

5. The relative size is correlated with the number of labials and rows of body scales, and these two characters —size and scutellation—constitute the only apparent specific differences, except in the few cases where they are accompanied by differences in color or relative tail-length.

6. The amount of dwarfing is not associated with particular geographic regions, but the scutellation and relative size of any form is that of its immediate ancestor plus the dwarfing which it has itself undergone. Thus a dwarf form of one group frequently occurs in the same region with a much less dwarfed representative of another group, the difference in relative size being due to differences in the number of forms between the one in question and the center of origin.

7. The variations in the characters of each form fluctu-

ate about a mean, and the transition in characters between the different forms is brought about by a gradual variation of the average type.

Students of evolution problems will recognize in this summary (*a*) the old story of the association of different forms with different environmental conditions, (*b*) the so-called definite or determinate evolution, and (*c*) that the phylogenetic variations are gradual.

It has long been noted that, among animals of the same group, the different forms are generally associated with different environmental conditions. In some cases it seems that these forms may occupy different habitats in the same environment, but in by far the greater number of instances, at least among terrestrial animals, directly related forms inhabit different, but neighboring, geographic areas. That there is some connection between the differentiation of such a group and the diversities of the region it occupies has usually been assumed; at least it is a fact that must be considered in any explanation of evolution. It is explained by natural selection on the assumption that the different conditions in the two regions demand different adaptations on the part of the organism, but this explanation will apparently not hold in the case of the garter-snakes, for there is certainly no advantage in dwarfing *per se*. It might be assumed (and it would be pure assumption) that this trait is correlated with unperceived adaptative characters, but this would seemingly be trying harder to save the theory of natural selection than to explain the facts. I have pointed out that there is no relation between the amount of dwarfing and particular habitats, but that forms (belonging to different groups) of quite diverse scutellation may occupy the same region. Apparently the conditions in each region do not call for a particular size (as would, it seems to me, be *approximately* the case if the struggle for existence in each habitat required that the forms become dwarfed), but only act to modify to some extent the invading form, the relative size of the latter being

determined as much by the modifications which the group has previously undergone as by those to which the particular form has been subjected.

I believe that these objections to the operation of selection in the evolution of these forms also argue against De Vries's mutation theory as an explanation, for, while it is easily conceived that mutations may have arisen within the limits of fluctuating variation in each case, we must also assume that the new form pushed into the new environment, or at least now occupies it to the exclusion of immediately related forms, because better fitted for it, which does not seem to be the case. What seems to have actually taken place is that as each group pushed out from the center of origin it became modified each time it encountered a new region of environmental conditions, not by the selection of forms better adapted to the new conditions, but by the modification of the entire section that invaded the new region. This may be tested more thoroughly by an examination of the method of evolution.

Perhaps the most striking characteristic of this genus is the manner in which evolution has taken place along definite lines. Although the forms frequently have other distinctive characters, they nearly all have this in common that they are more dwarfed than the form from which they have been derived, and there is no case in the genus where a form is larger than its neighbor toward the center of origin. The history of each group has thus been one of progressive dwarfing as it departed from the center of dispersal.

It is too often overlooked by students of evolution that natural selection can cause directed evolution (orthoselection); for in order that it may do so it is only necessary that there be an accruing advantage in the increased development of a character. The characters must thus be utilitarian, however, which is apparently not true in this case. Moreover, it would certainly be taxing the theory to make it account for the continued development

in the same direction in the four groups, when one considers the great variety of conditions with which they are associated. To explain this definite development on the basis of orthoselection it would be necessary to adopt the point of view that each form in each group found it of advantage in the struggle for existence in its particular environment to become more dwarfed than its immediate ancestor, which is to my mind unthinkable when one considers that we have in this genus four groups that push out in all directions from the center of origin, into desert, grassland and forest regions, in the tropical and temperate zones, and yet in every case the modifications associated with each region are practically of the same nature and non-adaptive. We meet the same difficulties if we attempt to apply the mutation theory to explain this definite evolution, for, while de Vries's mutants arise suddenly and are definite steps in new directions, he states in regard to the accumulation of characters:[4]

> It is not by mere chance that the variations move in the required direction. They do go, according to Darwin's view, in all directions, or at least in many. If these include the useful ones, and if this is repeated a number of times, cumulation is possible; if not, there is simply no progression, and its type remains stable through the ages.

It seems from this that in order to explain the evolution of a group by a series of modifications more or less similar in kind the mutation theory of de Vries is forced to fall back upon natural selection. If I have rightly interpreted the conditions, I believe that natural selection, with or without the assistance of the mutation theory, fails as an explanation of the definite evolution of this genus, and that we have here an example of true orthogenesis, *i. e.*, progressive modifications in each group without the aid of natural selection.

The nature of the variations is very interesting in several ways, and throws further light on the problem, for, although one must be cautious of forming conclu-

[4] De Vries, H., "Species and Varieties, Their Origin by Mutation," p. 572.

sions on this subject without the controlling evidence of experimentation, certain general relations seem to be apparent.

I have stated that the variations in each form fluctuate about a mean, but that this mean varies, approaching in the intermediate region that which characterizes the next form on its line of descent. That the different forms also originated in this way is shown in the numerous instances where they actually intergrade. This is essentially the idea of mutation (in the sense of Waagen and Scott) or "phylogenetic variation", which is not to be distinguished from individual variation by any character of quality or quantity, but by the fact that it pursues a determinate direction by the gradual shifting of the normal type. Conn[5] states that:

> It should be noticed that these considerations in regard to variations along definite lines have less significance in connection with such characters as can be supposed to advance by general averages. Some organs have been advancing in definite directions for long generations, but if the advance consists of an increase or decrease in size of the organs there is not needed any law of determinate variation to explain the matter. If it be an advantage to have an organ increase in size, and if variations in this organ occur around an average type, then without any necessity of supposing a special law directing variations, we can understand how natural selection will continue to increase the size of the organ in question.

All this is very true, for it is only orthoselection working on the average type, but as selection seems to be debarred in this case, the characters being non-utilitarian, we apparently have in the garter-snakes a case of evolution along fixed lines as the result of definite variation. Even if we could admit the selection of fluctuating variations as the dominant factor in the evolution of these forms, we should encounter the additional difficulty that it (selection) is apparently unable to create a new species, the form slipping back to the original condition when the selection ceases. The nature of the variations also seems to me to debar de Vries's theory of mutations as a

[5] Conn, H. W., "The Method of Evolution," p. 146.

possible explanation, for, according to de Vries, the specific changes are sudden and fixed, the new race appearing fully formed, which is certainly not the case in these snakes, unless we consider the new race as having been formed by small successive mutations of the same kind, which would, if I understand him rightly, be contrary to de Vries's idea of mutations, for he says that they "take place so far as experience goes without definite direction." We have apparently in these snakes an example of definite but gradual variation, in that there is in each group a gradual development of forms along a fixed path, without the aid of natural selection.

A theory that accounts for the definite evolution of this genus without the aid of selection is that there has been in each group a gradual modification of the forms under the influence of the environment. The determinate variation of the average type, the close association of the forms with different geographic regions and the consequent correspondence of areas of transition in characters with intermediate geographical conditions, would seem to render this conclusion unavoidable, if, as seems evident, selection is not operative here. It should be noted, however, that, while the evolution of the genus has been distinctly orthogenetic and associated with the environment, it does not appear that the latter has, as has often been supposed by adherents of this theory, a specific effect. This would be difficult to determine if we were dealing with one group, for example one that pushed northward from the Mexican plateau, for here there would be an increasing difference in climatic conditions, associated with accumulated modifications, between the range occupied by the form at the center and that of the most outlying species. But when all four groups are considered it is seen that the same modifications appear whether the group is pushing into the tropic or temperate regions, or into deserts, semi-arid plains, or humid forests, and it is difficult to conceive of environmental conditions common to all of the regions occupied

by these snakes that would exert such a specific effect upon them. It seems rather that throughout the genus the germ cells have such a restricted number of potential responses that the different groups have tended to vary in the same direction (homoplasy) under the influence of the environments which have been encountered; that is to say; the similarity of the response is conditioned by the constitution of the animal, the environment only acting as a stimulus upon the germ cells.

This theory would seem to satisfactorily explain why some directly related forms intergrade while others do not, for if infertility is in proportion to physiological diversity, as Darwin held, it is quite evident that as the new form produced as a group pushes into a new region becomes more or less modified, it will also probably become physiologically different from the parent stock and be more or less unable to cross back. This is essentially Eimer's Genepistasis, or Entwicklungstillstand, the standing still of certain forms at definite stages in development while others continue. But it should be noted in this case that the forms that progress each time are always associated with new geographic regions, and do not occur, as Eimer holds that they can, in the same region with the parent stock.

In conclusion I would like to point out that the purpose of this paper is to describe the method of evolution in the genus *Thamnophis* rather than to discuss the cause of the variations. It is evident that the suggested relation between the action of the environment and the nature of the response of the organism can only be tested by experimentation. I may add further that the interpretation offered of the conditions in this genus depends upon whether or not the relationships of the forms and the lines of development are as outlined. In pursuing work of this kind it soon becomes apparent that the relationships of any form can only be determined with certainty when the conditions that prevail throughout the genus have been examined carefully, and, conversely, that erroneous

ideas of relationships are very liable to result from incomplete knowledge of the course of evolution in the group, so that it is very hazardous to select a few forms of a genus and endeavor to discover the laws governing their development. An illustration can be drawn from this genus: *butleri*, which lies entirely within the range of *sirtalis*, may, so far as its characters go, easily be conceived to have been derived from the latter, and, if so, a different theory of the factors involved in its evolution must be sought to explain its origin. That it has more probably been developed from *radix* by dwarfing only becomes relatively certain when the lines of evolution in the genus have been worked out. This should discourage attempts to adduce as evidence for or against any theory the relationships of particular forms before the genus has been studied as a whole, and the general lines of development determined.

THE "PRESENCE AND ABSENCE" HYPOTHESIS[1]

DR. GEORGE HARRISON SHULL

STATION FOR EXPERIMENTAL EVOLUTION, CARNEGIE INSTITUTION OF WASHINGTON

IN Mendel's[2] discussion of the behavior of characteristics in the offspring of splitting hybrids, the phenomena of segregation are described in terms of pairs of antagonistic characters. He assumed that these are represented by pairs of internal units, one member of each such pair coming from one parent, the other from the other parent. This idea of pairs of characters in Mendelian hybrids has been generally entertained until somewhat recently, and is still perhaps not uncommonly held. De Vries[3] made use of this conception in stating what he thought to be a fundamental distinction between species and varieties, assuming that the differentiating features of varieties are represented by units which are homologous with corresponding units of the species from which such varieties sprang, and which are paired with those units on crossing, while different species lack such homology and pairing of determiners.

About six years ago in a paper on Mirabilis crosses, Correns[4] stated the members of several Mendelian "pairs of characters," as the presence and absence of *single* characters. Cuénot[5] in a paper doubtless written simul-

[1] Read before the Botanical Society of America, at Baltimore, December 31, 1908.

[2] Mendel, J. G. "Versuche über Pflanzen-Hybriden." *Verhandlung des Naturforscher-Vereines.* Brünn IV. 47 pp., 1866.

[3] De Vries, H. "Species and Varieties: Their Origin by Mutation," pp. 847, 1904. See p. 251 *et seq.*

[4] Correns, C. "Weitere Beiträge zur Kenntnis der dominierenden Merkmale und der Mosaikbildung der Bastarde." *Ber. d. deutsch. Bot. Ges.* **21**: 195–201, Ap. 23, 1903.

[5] Cuénot, L. "L'hérédité de la pigmentation chez les souris" (2me note). *Arch. de Zool. expér. et gén.*, **1** (4th S.): 33–41, 1903.

taneously with Correns's paper, but published several months later, used the same expression,[6] and most recent writers on Mendelian inheritance have adopted the method of presenting the characters in the terms of presence and absence.[7]

But while this change of usage has gradually taken place, little attention has been given to the real significance of the newer method of statement, except by Hurst,[8] who gives a good general discussion of the presence and absence hypothesis in a paper read before the Third International Conference of Genetics two years ago.

Hurst showed that of 44 Mendelian characteristics of various plants and animals studied by him, 41, or more than 93 per cent., can be appropriately described in terms of presence and absence. As one reviews these various characteristics, he can not avoid the feeling that in a number of cases the presence and absence could be read quite as well backward as forward, and it will doubtless be impossible in many cases to decide which is the positive character and which its absence. Thus in the contrast between a yellow and a green pea, the yellow is described

[6] Cuénot has not followed up the idea however in the development of a consistent usage, but continues to treat the supposedly antagonistic characters as if they are alike positive and represented by antagonistic internal units which he conceives to be the chromosomes. The idea that the chromosomes are the determiners of the Mendelian unit-characters has been also advocated by Spillman, but the latter appears to accept the correctness of the presence and absence hypothesis.

[7] Davenport considers "presence and absence" a relatively rare phenomenon. He says: "I think it is clear that dominance in heredity appears when a stronger determiner meets a weaker determiner in the germ. The extreme case is that in which the strong determiner meets a determiner so weak as to be practically absent as when a red flower is crossed with a white." (Davenport, C. B. "Determination of Dominance in Mendelian Inheritance." *Proc. Amer. Phil. Soc.*, 47: 59–63, 1908. See p. 63.) In papers which have come to hand since my paper was read at Baltimore, Bateson and his co-workers, and Castle have, on the other hand, declared unequivocally for the presence and absence hypothesis, as having general validity. See Bateson, Saunders and Punnett, "Experimental Studies in the Physiology of Heredity." Reports to the Evolution Committee of the Royal Society, IV. pp. 40, 1908, see p. 2, and Castle, W. E., "A Mendelian View of Sex-heredity," *Science*, N. S., 29: 395–400, March 5, 1909.

[8] Hurst, C. C. "Mendelian Characters in Plants and Animals." Report of the Third International Conference on Genetics, pp. 114–128, 1906.

as present in the yellow pea and absent in the green pea. What is to hinder us from describing the green as present in the green pea and absent in the yellow one? Similarly in the contrast between tall and dwarf, one could perhaps say "presence and absence of dwarfness on a tall basis" as appropriately as "presence and absence of tallness on a dwarf basis," and there seems no sufficient reason why the palm type of leaf in Primula should not just as well be considered a shortened fern type, as the fern an elongated palm type, or that the thrum is a shortened pin-eye quite as well as that the pin-eye is an elongated thrum. But notwithstanding such difficulties as these, there can be no question that most of the phenomena of Mendelian inheritance are more simply stated in terms of presence and absence than in any other way.

It has appeared to several writers as a difficulty for this hypothesis that in a number of cases what appears to be the absence of a character is dominant over its presence. There are a number of noteworthy cases of this kind. Thus, in cattle the hornless condition is dominant over horns; in most breeds of poultry white plumage dominates over colors and white legs over yellow legs; in snails unbanded shells dominate over banded, and less banded over more banded; in wheat, smooth heads dominate over bearded; in flowers having a yellow plastid color, white is dominant over yellow; in canary birds the presence of a mottled pattern is dominated by its absence, though in most cases color patterns are dominant over their absence. Thus in the mottled varieties of beans, for instance, the mottling factor is dominant over its absence, and in rabbits, the English-marked, Dutch-marked, tan-marked, tortoise-yellow, and agouti patterns are in each case dominant over their absence.

At several places Hurst states (*loc. cit.*) that the assumption that a certain character is the presence-character would "imply the dominance of that character," though in eight instances among the 44 he cites, he definitely places the absence dominant over presence. In

speaking of thrum and pin-eye Primulas (p. 122) he says:

> If we regard it as presence and absence of pin on a thrum basis this would imply dominance of pin over thrum in the zygote.

Again regarding the dominance of short hair over Angora in rabbits (p. 125) he says:

> If on the other hand we regard it as presence and absence of Angora on a short basis, this would imply dominance of Angora over short in the zygote.

Both Bateson and Davenport appear to have tacitly agreed that the dominance of absence over presence is a difficulty for the "presence and absence" hypothesis, for both have taken occasion to explain that what appears to be the absence of a character may really be the presence of a positive inhibiting factor. Indeed, Davenport[9] has taken the position that the positiveness of a character determines its dominance, and, therefore, all cases in which the absence of an external character dominates its presence must be explained by the existence of a positive factor in whose presence the given external character can not be produced. Thus, he says:

> A progressive variation, one which means a further stage in ontogeny . . . will be dominant; a variation that is due to abbreviation of the ontogenetic process, which depends on something having dropped out, will be recessive.

While I recognize the probability that there are positive inhibiting factors, as well as factors which produce specific structural and color characters, I think it can be shown that such an assumption is not necessary for the explanation of the dominance of the absence of a character over its presence. I will assume for the sake of the discussion that the presence and absence hypothesis is correct, and that the absence is real, having no internal unit to represent it. This assumption seems to me, as it did to Hurst, to be simpler and more practical than the alternative idea that the internal units are paired in the heterozygote, having a representative for absence as well as one for presence. I believe there is no fact on record[10]

[9] Davenport, C. B. Report of the Third International Conference on Genetics, p. 139, 1906.

[10] Except perhaps so-called "spurious allelomorphism."

which can not be as well explained on the basis of a single unit, as a pair of units.

On this basis the fundamental difference between the three classes of individuals produced by self-fertilization of a heterozygote may be simply stated thus: There are two classes of homozygotes, usually designated *DD* and *RR*, and the heterozygote, usually referred to as *DR*. The difference between the two kinds of homozygotes with respect to any unit-character is, that one—usually the *DD*—has one pair of allelomorphs or "genes"[11] in addition to those possessed by the other kind of homozygote—usually the *RR*. As the two kinds of homozygotes are often not appropriately called dominant and recessive, I will call the one which has the added pair of genes (*i. e.*, the one which has $2n+2$ genes) the "positive" homozygote, and the one which lacks them (*i. e.*, the one with only $2n$ genes) the "negative" homozygote. If we designate collectively the common features of two parents which differ from each other in a single unit-character by the letters *BB*, and the differentiating genes by the letter *A* repeated as often as the gene is repeated in each nucleus of the soma or sporophyte, the positive homozygote will have the composition *AABB*, the negative homozygote will be simply *BB*, and the heterozygote will be *ABB;* and whatever differences are observable in these three classes of individuals must be due obviously to the presence of none, one, or two "*A*" genes in each nucleus and to the reactions of these with the underlying factors which have been here collectively represented by "*BB*."

In order to see the bearing of these assumptions upon questions of dominance we must consider briefly the nature of the unit-characters. Regarding the nature of the genes themselves—the primary character-producing

[11] This word is proposed by Dr. Johannsen as a substitute for words such as pangenes, ids, allelomorphs, etc., which have been used to denote an internal something or condition upon whose presence an elementary morphological or physiological characteristic depends. The word "gene" has the advantage that it does not assume by its form or derivation any hypothesis as to the ultimate character, origin or behavior of the determining factor.

units—I have nothing to suggest, for to that question I am, like Professor Bateson,[12] inclined "to hold my fancy on a tight rein;" but there can be no doubt that the *visible* Mendelian characters are always secondary, and but little doubt that they are all dependent at some stage of analysis upon chemical relations.

This is too obvious to need discussion in the case of color-characters, and in those structural characters which involve only some by-product of the metabolism of the cells as, for instance, the starchy or sugary character of the endosperm in maize. It requires perhaps a more daring flight at present to assert that such structural characters as hairiness, branching, lobation and serration of leaves, production of horns, extra toes, different forms of comb, etc., which involve the number, direction and succession of cell-divisions, depend likewise upon the intimate chemical nature of the protoplasts; but even if it could be shown that *physical* properties of the protoplasm are to a certain degree determining conditions of cell-division, the resulting structures could hardly conceivably be permanent hereditary features, unless these physical properties are dependent at last upon the chemical composition of the protoplasm.

Having arrived at the conclusion that all the Mendelian characters are dependent upon chemical relations, we may return to the question of dominance, and the relation between the two kinds of homozygotes and the heterozygote, and see to what extent the known facts may be interpreted in terms of chemical experience.

A fundamental principle in this connection is the law that the extent of a reaction between two chemicals is determined by the amount of that reagent which is present in less relative quantity, and not by the one which is present in excess. When the positive homozygote, *AABB*, and the heterozygote, *ABB*, are alike, *i. e.*, when there is complete dominance of presence over absence, it

[12] Bateson, W. The Methods and Scope of Genetics. 49 pp., Cambridge, The University Press, 1908. See p. 12.

may mean that already the presence of the one unit *A* of the heterozygote is sufficient to result in the maximum reaction, in which case the doubled factor *AA* of the positive homozygote can do no more. When, on the other hand, one unit *A* is not sufficient to produce a maximum reaction with the other factors present, the *AA* of the homozygote produces the corresponding character in greater intensity, and the heterozygote will be intermediate between the two homozygous parents. Both of these conditions are frequently realized.

The case I have wished to deal with specifically is that in which the heterozygote—the *ABB* individual—does not differ in external aspect from the *negative* homozygote, *BB*, so that the ratio becomes 1:3 instead of 3:1, this is the situation in which the absence of a character is dominant over its presence. In such a case the character determined by *A* is latent in the heterozygote. To show that this situation is possible it need only be pointed out that in a number of familiar instances a precipitate is formed or some other visible reaction takes place only in the presence of a certain excess of one of the reagents. It is perfectly clear that in any such case, one may add nearly enough of the reagent which is required to be in excess, and no apparent reaction will take place, but if the quantity of this reagent be doubled the characteristic reaction will occur. Now this is just what I conceive may take place in certain crosses. In the heterozygote where the chemical unit *A* (of whatever nature) occurs but once in each nucleus, no reaction becomes apparent, but in the pure-bred forms bearing the unit *A* in double quantity, *i. e.*, *AA*, the specific character (or reaction) produced by this unit appears. The heterozygotes will then be indistinguishable from the negative homozygote, and in the offspring of two heterozygotes bred together there will be among every four individuals on the average three which have the character absent and one which has it present, or in other words "absence will be dominant over presence."

Very neat laboratory experiments can be arranged to illustrate this behavior, with any reaction in which a certain excess of one of the reagents is required, and while these reactions will probably be in most cases of much greater simplicity than those presented by the interaction of the hereditary units, and they can, therefore, be considered only as presenting analogies, I am convinced that such analogies are not unfair ones.

It is especially easy to arrange an experiment showing such a result in the case of certain organic substances known as indicators, as litmus and phenolphthalein, for here one needs to assume only that the single, unpaired unit in the heterozygote produces such a quantity of acid or alkali as will not quite change the character of the cell-sap of the negative homozygote with respect to acidity or alkalinity. Thus if I make an alkaline solution of litmus and add to it as the product of one assumed unit, *A*, such a quantity of any acid as leaves the solution still slightly alkaline, I may allow this to represent the heterozygote. Then the homozygote possessing the acid-producing unit *A* will have it in double quantity or intensity. When I add this second portion of acid to the solution it is instantly changed from alkaline to acid, as is indicated by a change from blue to red color. The negative homozygote lacking the acid-producing unit and the two heterozygotes are alike blue, while the individual which is pure with respect to this unit whose specific external manifestation is the production of a red color, alone possesses that character, and this results in a realization of the ratio, 3 absences to 1 presence, or the dominance of absence over presence. This example has the advantage of being conceivably duplicated in the case of many vegetable color-characters, for the very widely distributed anthocyan which gives the red and blue colors is an indicator similar to litmus, and could have been used in this experiment instead of litmus.

Whether the situation here outlined is actually attained in the case of red and blue flowers in nature can not per-

haps be demonstrated. It is the general experience that blueness is dominant over its absence, but this is just the result I have pictured here as a case in which absence of redness or of acidity is dominant over its presence. I know of no way of determining whether red flowers are blue flowers with an added factor for acidity, or whether blue flowers are red with an added factor for alkalinity, and, indeed, it is conceivable that both of these situations may be presented in different species. However, my purpose is attained if I have shown that there is no greater theoretical difficulty involved in the dominance of absence over presence than in the dominance of presence over absence, and that the assumption that any given character is due to the presence of an added internal unit does not "imply the dominance" of that character.

The non-appearance of an externally visible character in the heterozygote, although the corresponding internal unit is present, as must always be the case when real absence is dominant over presence, plainly presents a kind of latency somewhat different from the four types recognized by me[13] in a recent article in the AMERICAN NATURALIST. For the sake of uniformity with the terminology there adopted I may call this new kind of invisibility "*latency due to heterozygosis.*" Like all the other types of latency except that due to fluctuation, the latency resulting from heterozygosis produces no deviation from definite characteristic ratios.

I recall at present only one case in which we can certainly identify latency due to heterozygosis, for the reason that, just as we have seen above in regard to blue and red flowers, it may be quite impossible in any particular instance to decide which is the positive character and which its absence. In a particularly interesting cross between a yellow and a reddish snail, Lang[14] has found

[13] Shull, G. H. "A New Mendelian Ratio and Several Types of Latency," AMERICAN NATURALIST, 42: 433–451, July, 1908.

[14] Lang, A. Ueber die Bastarde von Helix hortensis Müller und Helix nemoralis L. Eine Untersuchung zur experimentellen Vererbungslehre. Jena: G. Fischer. 1908.

that the heterozygotes are yellow when young and red when they grow older. In this case the appearance of yellow in the young stage leaves no doubt that this is the fundamental color upon which the red is superposed. The pure bred red snail—the positive homozygote—is red from its earliest stages. This latency of the red character in the young heterozygotes produces a dominance of the absence of red over its presence in the early stages of development, and if the snails are classified at this time, the F_2 is found to consist of 3 yellows to 1 red. Later in life the heterozygotes become red and the census shows 3 reds to 1 yellow.

The rather frequent occurrence of heterozygotes lacking the usually dominant character may be quite appropriately said to present cases of latency due to the combination of fluctuation and heterozygosis.

Summary

The "presence and absence" hypothesis assumes that what appears to be a pair of characters in Mendelian inheritance is really the presence and absence of a single character. This hypothesis has now won the support of most of the leading experimental students of heredity. The fact that the absence of certain characters dominates over their presence has appeared to some to be a difficulty. This paper shows that no such difficulty is involved and simple chemical experiments are cited which, if duplicated among plants and animals, as they no doubt are, would give the dominance of absence over presence, without recourse to "inhibiting factors."

When absence dominates over presence the positive character is latent in the heterozygote. Such cases may be said to show *latency due to heterozygosis*. This condition is exemplified by some of Lang's snail crosses. The same phenomenon is involved in many cases of failure of dominance in heterozygotes.

Station for Experimental Evolution,
Cold Spring Harbor, L. I.
December, 1908.

PRESENT PROBLEMS IN PLANT ECOLOGY[1]

III. Vegetation and Altitude

PROFESSOR CHARLES H. SHAW

The Medico-Chirurgical College, Philadelphia

In the study of the relation of plants to environment, there are few problems of greater interest than those presented by the vegetation of mountains. The general facts are somewhat familiar, and reference to them is here necessarily brief. Whatever the vegetation of the surrounding country, mountains are usually forested; the forest is often composed of several zones in which different kinds of trees successively predominate; higher up the forests finally cease and give place to grassland of perennial herbs and low shrubs—these are some of the more general facts of mountain vegetation. There is bound up with them not only strangeness and beauty, but also a series of most interesting problems in the ecology of plants.

If I understand rightly the reason for this symposium, my duty is to state, as well as in brief compass I may, the present state of our knowledge in regard to these phenomena. In general, they rest back upon physical environment. In so saying, however, it must be kept in mind that biotic factors early modify the primitive physical ones; the reason for the occurrence or absence of a species may be the conditions created by other species.

The important factors which vary with altitude seem to be heat, light, precipitation, evaporation, and a factor made up of several of those named, namely, length of season. Let us consider these severally, and try how far

[1] A series of papers presented before the Botanical Society of America, at the Baltimore meeting, by invitation of the council.

we may at present determine the part played by each in connection with the plant life of mountains.

1. *Heat.*—From the days of Humboldt to the present, the vast importance of temperature in this connection has been recognized. In spite of this, our knowledge is rather scanty and vague. It has been usual to attribute great importance to the severe cold of mountain tops. This view, however, is entirely open to challenge. Mountains which rise up from warm plains certainly can not be invaded by plants which are killed by frost, but is there warrant in any physiological knowledge we now possess for supposing that extreme low temperatures are of any especial significance for plants which endure freezing? There is reason for believing that some woody plants are cracked by severe cold, but I believe the general question must be answered in the negative. That treeless mountain tops are not so because of great cold is shown by two facts: First, in cases that have been investigated, timber lines do not bear any direct relation to isothermal lines; and furthermore, forests do exist in the coldest districts on the globe. Herbaceous plants, too, taken even in the active condition, are known to survive extremely low temperatures, undisturbed.

We may note in passing the obvious fact that, for most low growing mountain plants, deeply buried as they are under snow, extreme winter temperatures do not come in for consideration at all.

That the lower temperatures of air and soil during the growing season are factors of great importance is not to be doubted. More specific information is not easy to obtain. Direct observation avails nothing, for we can hardly point to a single feature of anatomy or histology which is called forth by or conditioned upon heat or cold. In order to make further progress, recourse is naturally had to instrumental study. In the use of this method, many pitfalls await the worker. It is relatively easy to secure data of temperature, but *vastly difficult to interpret them.* It seems to me that, seeing a good

many ecologists are making use of temperature data, this point will bear some emphasis. Feeling that ecology is new, and exact instrumental work is the kind that counts, it is very easy, when one has secured a fine series of readings, or better still, a complete thermographic tracing for a growing season, to entertain the impression that he has accomplished something of note; whereas the fact in the matter simply is that if he has done his work well, it is of a quality with the routine work of a weather bureau. To relate the physical data to the manifold activities of a living plant is another matter, and calls for all the power of critical thought and all the knowledge of physiology which any man can command.

For our purpose, it seems possible to do little more than to point out some difficulties to be surmounted. To begin with, any method which assigns increasing values to higher temperatures must go astray as soon as the plant's optimum is passed, and for most of the plants we are dealing with, we do not know where that is. If, also, as there is some reason to believe, the growth-temperature curve has more than one maximum, a still further difficulty would be brought in.

Furthermore the ecologic optimum is made up of many harmonic optima, and may vary in different life phases of the same plant. In experiments in forcing fruit trees, it has been found that the optimum for blooming is markedly lower than for other periods for the plant's activity. Finally the temperatures recorded are for the soil or air, whereas the ones wanted are those that prevail within the plant. Leaves and shoots are warmed by sunshine and cooled by the evaporation of water. In this way temperatures may be brought about which differ materially from those recorded by a thermometer alongside. In the case of an Alpine plant, sheltered in some sunny angle of rock, how widely the temperature within its leaves may differ from that shown by a thermometer near by, properly set up for air temperatures in shade!

On the positive side, there seems less to be said. It

can not be doubted that the plant life of mountains is in no small degree modified and controlled by temperature, but who can put his finger on definite facts and say "this temperate forest is on this mountain in the tropics because of temperature," or "this Alpine plant is a dwarf because of cold." Strongly as we may suspect such points, we must be cautious about including them within the realm of our positive knowledge.

The peculiarities of Alpine plants have been thought to be due, in part, to great daily variation in temperature; that owing to the greater clearness and rarity of the atmosphere, the plant is more exposed to heating by intense sunshine by day, and cooling by more rapid radiation at night. Since growth takes place particularly at night, it seems evident that marked night cooling would lead to reduced size. That this is actually true has been proven by placing growing plants each night in the ice chest. At present more light is chiefly needed as to what temperatures are really experienced by Alpine plants over night. Air temperatures, at any rate, are more equable at high altitudes. In connection with the work in the Selkirks during the past summer, two complete thermographic records were taken, one meter from the surface, same hillside and exposure, at altitudes of 800 m. and 1,700 m., respectively. The daily maxima recorded at the upper station were notably less than at the lower; the nightly minima only slightly so. (Freezing point was not recorded for many weeks.) Such data accord well with the general results of meteorologists. They refer of course only to air temperatures.

Briefly summarizing, we may say that our knowledge of the relation of heat to mountain vegetation is not great. The importance of extreme low temperatures has been much overestimated. The significance of moderate temperatures is not yet capable of exact interpretation. The hypothesis of night cooling as a cause of alpine dwarfing needs further physical facts as a basis.

2. *Precipitation.*—That mountains are islands of

greater precipitation and that the vegetation of mountains is largely dependent upon atmospheric water are ideas familiar to every one. Schimper has further suggested that light showers at high altitudes favor the development of grassland rather than forest. This idea, to be tenable, requires the further assumption that the soil in the grassland zone is deficient in water supply. This may be true for lower latitudes, but it scarcely seems admissible for northern mountains where the late melting snows leave the soil supplied with all the water it can hold.

In quite a different way, too, precipitation in the form of snow becomes a decisive factor for vegetation. In a paper read before this society, a year ago, I showed that the timber line of the Selkirks was due to the heavy snow beds at those altitudes. By a coincidence, Cowles showed elsewhere, at the same time, that in a number of places in North America snow beds and timber line were causally related.

3. Closely connected with the question of heat and precipitation is another factor of prime importance in some mountains, namely, *Length of Season.*

In respect to this factor at least two points of view are necessary. For trees and plants growing on wind-swept spots, length of season is a question of temperature. For the vast majority of low-growing plants, on the other hand, length of season is also a question of emergence from snow beds to air and sunshine.

Taking up, first, the question of forests, it has been said that the total heat available at high altitudes is not sufficient for the maturing of new wood, and more particularly, that the season is too short for the ripening of good seed. Both of these ideas must stand or fall simply upon evidence, and so far as I am aware, none of a reliable character has been brought forward. It may be remarked that seedling trees usually seem abundant enough at timber line. It would be of interest to gather seeds of balsams, etc., growing at timber line and learn

if they germinated properly. When one considers the fact that elevated forests are usually coniferous, Myake's studies on photosynthesis by evergreen trees during winter become of interest. One may well inquire if trees of this kind obtain in this way a distinct advantage over others at high altitudes.

Turning to the low growing plants, we find their problems of a somewhat different nature. In the Alps, the Caucasus, the northern Rockies and the Selkirks to mention only a few examples, large tracts of lofty grassland lie buried under snow until the close of the vernal period. If one visits the higher forests of the Selkirks in June, he must journey in the snow. Arriving at the alpine fields, he finds them at the summer solstice, still hidden under an almost unbroken covering of white. In the month that follows, they will be gradually exposed. During the ten or fifteen weeks that remain, they must accomplish nearly the whole sum of their annual activities. The ability to do this must be a decisive factor in their struggle for existence. *Carex nigricans* ordinarily occurs mingled with other plants; but in moist hollows, where the snow has lingered until the middle of July, it often forms patches to the entire exclusion of competitors. Where the snow does not melt till the first of August, it is absent and the visible vegetation consists of polytrichum only. Where snow persists till late in August, the soil thus exposed is destitute of visible vegetation. Walking in the verdant alpine fields at the end of August, one finds each unmelted patch of snow bordered by plant societies in the order mentioned. Do we not read in this that of phanerogamous plants present the sedge is best able to compress its life processes into a brief period; that the moss is able to live with even shorter time allowance, but that even the moss is unable to maintain itself under conditions of such brevity of season as are represented by twenty or thirty days at the close of summer? It is hardly to be doubted that many other less easily traced questions of association and occurrence are decided by length of season.

4. *Light.*—Since a certain proportion of light is absorbed during passage through the atmosphere and particularly by the layers next the earth's surface, it seems plain that light becomes more intense with increasing altitude. If so, its relation to vegetation is a matter of much interest.

Notwithstanding that the question has received considerable attention, our knowledge of it is still in a rather unsatisfactory condition as will appear from the following:

Bonnier, Schimper, Schroeter and indeed most of those who have written upon the subject, express the belief that the more intense light is a factor of importance in connection with Alpine vegetation. They give reasons indicating that a greater intensity exists, and noting the reduced leaves and shoots and prominent flowers of alpine plants, state that the former is the cause—in part at least—of the latter. The conclusion, however, has not been put to the test of discriminating experiment.

Any further discussion of the subject brings in a general consideration of light as an ecological factor. I trust a brief digression may be permissible.

Since light is a form of solar energy, efforts have naturally been made to compute its intensity from astronomical data. Attempts have been made in several quarters to calculate light intensity for any day and hour of sunshine for the year at a given latitude. They do not, however, seem to have been happy in escaping fundamental error. For, in making calculations from the sun's altitude, there is not one varying factor, but several which must be reckoned with: (1) The amount of radiant energy falling upon a horizontal surface varies with the sine of the sun's altitude. This law is perceived by every one. It has sometimes been neglected, in the thought apparently, that since leaves stand at all angles, it is unnecessary to reckon what a horizontal surface may receive. Yet the direct light available for the total vegetation of a hectare or any other area is func-

tioned upon the angle made with the sun's rays. The law of the sine may, therefore, not be neglected. (2) Within the atmosphere we have the phenomenon of diffuse light from the sky. At the earth's surface it becomes a factor of no small importance, very likely surpassing for vegetation in general that of the direct rays of the sun. It is, of course, derived from direct light, but for it the law of the sine is far from valid. In general, it is subject to less variation. It is probably affected by many factors not easily observed, presence of dust, vapor, etc., and its numerical computation borders on the impossible. A table showing light intensity for any given day or hour, might possibly, if all factors were taken into account, show the value of direct light, but it is open to question, if this is what the botanist chiefly wants to know. (3) The length of the path of a ray of light through the earth's atmosphere, and, therefore, the fraction of it which is absorbed, increases with decreasing elevation of the sun. Quite apart from diminution due to decreasing angle of incidence, the light wanes as the sun approaches the horizon. This fact is sometimes clearly seen; sometimes apparently overlooked. (4) Absorption in the lower, denser, dust, water-vapor and carbon dioxide bearing layers of the atmosphere is relatively far greater than in the upper and rarer ones. This last holds good, especially for the shorter rays. This third consideration comes to the foreground in a study of altitude and vegetation.

Here then are several varying factors; some of them difficult to calculate, and none of which may be neglected. Moreover, as will be shown below, there is reason for doubting whether any theoretical calculations are valid, even for clear days.

Wiesner has carried on extensive studies upon light and plants, extending over several decades. He offers data to prove that light, for a given time and place, with cloudless sky, can by no means be calculated from astronomical data. His readings taken in different parts of

the world show astonishing irregularities. In Buitenzorg, the light diminished rapidly between eleven and twelve o'clock under apparently clear sky. Similar data were recorded for Cairo, Egypt. The maximum intensity obtained anywhere in the world was not in the tropics, but in Yellowstone Park. Though some of his results seem rather incredible, it must be owned that his methods appear ample and critical—far beyond anything else undertaken by a botanist. He has emphasized the distinction between direct and diffuse light. He finds the proportion of the former to increase greatly with altitude, and sees in this a factor of much importance for vegetation. His results in regards to altitude and light are not so full as could be wished, but he attributes the maximum observed in the Yellowstone to altitude, and, in general, assigns a high importance to light as a factor in alpine climate.

On the other hand, Clements states that in Colorado the variation of light with altitude amounts to a very small percentage and concludes that such differences as exist are too small to receive serious consideration in a study of mountain vegetation. The chief thing, therefore, that appears certain is that the whole question is in an unsatisfactory condition. In such a situation, one or two points must be kept clearly in view.

First, data as to light intensity must be obtained by methods which will pass muster with physicists. A certain body of such data are available. Time is lacking to take up the question here, but the work of Cayley, Violle, Langley and others might be cited to show that a considerable increase in light intensity with altitude does exist.

In the second place, it must be borne in mind that the relation of the plant to light is a complex one. In some of the work above quoted there seems to be the wholesale error of assuming that the importance of light for the plant is to be judged by observation upon its relation to the process of photosynthesis. It seems super-

fluous to emphasize that light is not only a source of energy, but a factor which now stimulates, now inhibits various activities of the plant in a profound degree.

It is the highly refrangible rays which suffer greatest absorption by the atmosphere. The light at the surface would, therefore, differ in *quality* from that at higher altitudes. In studying the question, it appeared to me desirable to learn whether any responses by plants could be found to alterations in quality—alterations, nevertheless, in which all kinds of rays should still be present. I therefore endeavored to set up experiments which should merely add a proportion of certain rays to an already sufficient daylight illumination. The results, while far from being as full and conclusive as could be wished, seem to indicate pretty clearly that plants do respond to such a variation in quality. Internodes were observably shorter and leaves more hairy under the bluer light.

Perhaps the whole question can be summed up in saying that the relation of vegetation to variations in light due to altitude are poorly understood; that more data from trained physicists would be welcome, but that the experiments still remain to be made which would enable us to interpret such data with confidence.

5. *Evaporation.*—Since pressure becomes less, wind velocity increases, and insolation becomes greater with increasing altitude, it has seemed necessary to conclude that the evaporation rate increases. Toward the summits of many mountains, *e. g.*, the White Mountains and Adirondacks, the decisive relation of wind to forest vegetation can hardly be doubted. In these cases there is good ground for assigning evaporation as the cause of timber line with all that it involves. The death of buds and twigs is probably chiefly due to drying in cold weather.

Most of the leading writers agree without question that evaporation is more rapid at higher altitudes. Schimper lays much emphasis upon it; Schroeter writes vividly of the drying of skin experienced by alpinists

and mentions the dry cured meat prepared by peasants in some places in the Alps, which, it is stated, is due to the greater drying power of the air. The reasoning is all but conclusive. There can be no doubt though, that the verdict of the soundest reasoning ought to be confirmed in the court of experimental evidence.

In 1907, Livingstone measured evaporation in the Santo Catalina mountains and found a *decrease* with altitude. This, perhaps, was not surprising, seeing that the series began in the desert below and extended to the cool mountain regions above.

During the past summer, I set up two series of instruments in the Selkirks at altitudes ranging from 800 m. to 2,900 m. Mountain flanks having a fairly uniform exposure were chosen, only short horizontal distances were involved, two stations were chosen at each altitude so that one might check the other. The season was favorable, being unusually warm and dry; one series was in perfect operation for twelve weeks. The results on the whole seem to exclude the idea that in the Selkirks evaporation increases with altitude. The maximum in each case was at the next lowest station, altitude of 1,100 meters. Above that there was a gradual and irregular diminution. It may be that the lower temperatures of higher altitudes more than offset the factors which make for increased evaporation. Indeed, it appears certain from the above data that for the Selkirks, such is the case.

The data in question, however, present only weekly totals. The possibility that excessive evaporation may take place during certain portions of the day, still remains to be studied. It must be ever kept in view, too, that it is not the absolute amount of transpiration which is so much of importance to the plant, as the balance between water supply and water loss. If the lower soil temperatures of higher altitudes make the obtaining of water more difficult, then the same or even a diminished evaporation rate might demand increased power of resistance on the part of the plant.

In trying to unravel the problems of mountain vegetation, it must never be forgotten that the plants of the present are descended from preexisting ones; facts of heredity are everywhere; phenomena that are found today not seldom hark back to conditions of the past.

In concluding, allow me to offer a plea for a service, which I have been thinking for several years would be one of the most helpful which could be rendered to this adolescent science of ecology, namely, that some one whose knowledge of physics and physiology fits him for such a task should overhaul and scrutinize our ideas and methods. Not counting minor and ephemeral papers, there can be no question that ecology, at the present time, contains not a little of discernible error. Rumors have been heard that zoologists are beginning to study ecology and looking to botanical methods for hints for developing their own. Within the family, it may be said that if wide-awake guests are coming, it is time to set the house in order. Moreover, ecology is finding a large place in elementary text-books, and in this way errors are being propagated. The interest alike of science and education in this field could in no way be better served than by a relentless pruning.

DISCUSSION OF PROFESSOR SHAW'S PAPER.

DR. LIVINGSTON: A remark was made by Professor Shaw in the beginning of his paper, which suggests that we sometimes lose sight of physical facts. A certain plant is not killed or shut out by the fact that other plants are near it, but by the fact that light conditions or moisture conditions or evaporation conditions or temperature conditions are different from those in which they might live. It seems to me that to speak of biotic and physical conditions leads to confusion; the thing the plant feels must be a physical thing.

PROFESSOR SHAW: In my remark I meant to clear up certain cases where one might lose sight of the fact that plants had largely modified physical conditions. I presume the very case which gave rise to that sentence was this: there are some reasons for supposing that in the Selkirks, the zone of greatest moistness, where lichens and mosses flourish is at something like 4,000 feet in altitude. A forest has developed there, and the condition of low evaporation rate has come about on account of that forest.

SHORTER ARTICLES AND CORRESPONDENCE

PLEISTOCENE SWAMP DEPOSITS IN VIRGINIA

Buried swamp deposits of Pleistocene age are far more abundant in the Atlantic coastal plain than was suspected a few years ago. A large number of such deposits are exposed by the comparatively recent cutting of the waves along the western shores of the Chesapeake Bay and the estuaries of our southern rivers. These deposits vary greatly in botanical interest from point to point. In some no recognizable remains have been found, in others these are limited to the stumps of the cypress, while still others contain the remains of a considerable flora. It seems evident that quite a number of modern species are more restricted in their northward range than they were during certain interglacial periods or even post-glacial time, while others are extending their range at the present time. Among the former the red bud or Judas-tree (*Cercis canadensis* Linné) and the osage orange (*Tokylon pomiferum* Raf.) might be mentioned, both occurring in the interglacial beds of the Don Valley near Toronto in Canada. Another species abundant as far northward as New Jersey in inter- or post-glacial time was the bald cypress (*Taxodium distichum* Rich.), and the loblolly pine (*Pinus taeda* Linné) also appears to have withdrawn southward since the late Pleistocene. The water elm (*Planera aquatica* Gmel.), on the other hand, appears to have retreated southward in the late Pleistocene and to be readvancing at the present time.

Numerous Pleistocene swamp deposits are described in the recently published account of the Maryland Pleistocene[1] and their contained fossil plants have been admirably exploited by Dr. Hollick, who enumerates over 40 species from beds of this age in Maryland.[2] Similar deposits are to be found at many points in the Old Dominion, although very little attention has been thus far devoted to their description.

In 1906 the writer described[3] *Fagus americana* (nuts) Vitis sp. (seeds), *Hicoria glabra* (fruit), *Taxodium distichum* (seeds

[1] Maryland Geol. Surv., Pliocene and Pleist., 1906.

[2] *Ibid.*, Systematic Paleont., pp. 217–237, pl. 67–75.

[3] Berry, *Torreya*, Vol. 6, pp. 88–90, 1906.

and cone-scales) and *Nyssa biflora* (seeds) from the Talbot or latest Pleistocene formation at Tappahannock, Va.

During the last two years peat deposits of late Pleistocene age have been discovered at numerous points along the Potomac, Rappahannock and James rivers. These usually contain characteristic stumps of the cypress, often of large size, and the associated peat furnishes recognizable plant remains, generally seeds, of Nyssa, Vitis, Fagus and Taxodium, the latter usually the most abundant. Associated with the plant remains are fragments of the elytra of beetles, occasional insect galls and molluscan remains. Evidently most of these Pleistocene peats indicate the presence of cypress swamps, but this is not always the case, since in some instances we find representatives of upland vegetation, while in other cases the fossils show that the vegetation was open and marsh-like with a scattering of trees of oak, birch and pine. Where quiet water conditions followed the subsiding forest-bed, deposits of clay are to be found and these often contain fragments of leaves along with casts of the shells of Unio if the locality is toward the head of the ancient estuary, or shells of *Rangia cuneata* if the waters were more saline. The latter is very abundant in Pleistocene deposits of this sort from Maryland southward and it is also a member of the modern fauna, confined, however, in the latter case to the Gulf of Mexico.

Fig. 1 shows the bed of massive hard peat a short distance above Tappahannock, Va., from which the above mentioned species were collected. It is exposed for a thickness of four or five feet and shows many cypress stumps in place with the "knees" protruding through the recent narrow sand-beach. Overlying the peat is a layer of drab plastic clay from one to four feet thick and carrying fragments of leaves. Above this there is from ten to fifteen feet of coarse sand. The Rappahannock has cut into the bluff along its south bank, exposing this old cypress swamp for a distance of over one half a mile.

Where the forest-bed was succeeded by waters which were agitated by wave action or swift currents the overlying deposits are sands or gravels laid down on the more or less planed surface of the old swamp. Fig. 2 shows such a condition of affairs in an exposure just above the junction of Parrotts Creek with the Rappahannock River. The line of apparent unconformity is sharply defined running across the center of the picture. Below are seen the cypress trunks and roots embedded in an impure peat which was planed off by wave or current action as the

FIG. 1. Talbot Cypress—Swamp near Tappahannock, Virginia.

FIG. 2. Talbot swamp deposit just above junction of Parrotts Creek and the Rappahannock River.

swamp subsided. Upon this surface lie the coarse sands shown in the upper half of the photograph.

The additions to the Pleistocene flora of Virginia are enumerated below. Those from below Port Royal were collected by Dr. L. W. Stephenson, of the U. S. Geological Survey, who has also kindly furnished the two photographs here reproduced.

FAGALES

BETULA NIGRA Linné.

Knowlton, *Amer. Geol.*, vol. 18, p. 371, 1896.
Berry, *Journ. Geol.*, vol. 15, p. 341, 1907.
———, AMER. NAT., vol. 41, p. 692, pl. 2, figs. 2–4, 1907.

This riverside and flood-plane species appears to be abundant in the swamp deposits of our southern coastal plain, due doubtless to its abundance along the rivers which contributed their flotage to these deposits. The present occurrence is based upon leaves from the right bank of the Rappahannock River one and one half miles below Port Royal.

QUERCUS sp.

A number of fragments of leaves, evidently those of some oak but too fragmentary for even tentative specific determination, are contained in the collection from the right bank of the Rappahannock River one and one half miles below Port Royal, and undeterminable acorns occur in the Talbot deposits near the Nomini Cliffs on the south shore of the Potomac.

FAGUS AMERICANA Sweet.

Hollick, Md. Geol. Surv., Pli. and Pleist., p. 226, 1906.
Berry, *Torreya*, vol. 6, p. 88, 1906.
———, *Journ. Geol.*, vol. 15, p. 341, 1907.
———, AMER. NAT., vol. 41, p. 692, pl. 2, fig. 7, 1907.
Fagus ferruginea Michx., Lesq., *Am. Journ. Sci.*, vol. 27, p. 363, 1859.
———, Geol. Tenn., p. 427, pl. 7 (K), fig. 11, 1869.
Fagus ferruginea Ait., Knowlton, *Amer. Geol.*, vol. 18, p. 371, 1896.
Mercer, *Journ. Phila. Acad.* (11), vol. 11, pp. 277, 281, fig. 8 (15), 1899.

The characteristic leaves and burrs of this species occur in the Talbot deposits near the Nomini Cliffs. No nuts were found associated with the other remains, but an extended search was not made. This species was one of the commonest trees of the Pleistocene if we may judge from its abundant remains at a large number of localities in Pennsylvania, Maryland, Virginia, West Virginia, Tennessee, North Carolina and Alabama.

CELTIS OCCIDENTALIS Linné.

Bony endocarps, or stones, sometimes enclosed in the lignitized

exocarp, and not distinguishable from those of the modern tree, occur in the peat deposits near Tappahannock. In the modern flora this wide-spread species ranges from the Atlantic to the Pacific and from southern Canada to eastern Texas and Florida. It has not heretofore been recorded in the fossil state. The genus dates back to the middle Eocene in this country, but it is not abundantly represented at any horizons. Leaves described as *Celtis pseudo-crassifolia* by Hollick[4] occur in the older Pleistocene (Sunderland) of Maryland. Abroad the genus is commonly represented in the late Tertiary, at least two species being recorded from the Pliocene, but none so far as the writer is aware from the Pleistocene.

SPINDALES

ILEX CASSINE Linné.

This species which in the modern flora is a denizen of low woods and river banks near the coast from Virginia to Florida and west to Louisiana has not heretofore been found fossil. Eight specimens of leaves are in the collection from the right bank of the Rappahannock River one and one half miles below Port Royal. They are identical with the less elongated leaves of the modern plant and would seem to indicate, if their habitat has remained unchanged, that the Talbot coast line was much farther to the west of where it is to-day, a fact fully borne out by the areal distribution of the deposits of the Talbot Sea. They also show that in Talbot time this species ranged somewhat farther north than it does at the present time, since southern Virginia marks its present northern limit according to Sudworth.

ERICALES

DENDRIUM PLEISTOCENICUM Berry.

Berry, *Journ. Geol.*, vol. 15, p. 346, 1907.

Leaves of this species described originally from the Pleistocene of central North Carolina are present from one and one half miles below Port Royal on the Rappahannock River. They are considerably smaller than the North Carolina leaves, but are identical with them in outline and venation and they are also very similar to the leaves of the existing *Dendrium buxifolium* (Berg.) Desv. As previously pointed out, they probably represent the ancestral form from which the modern upland species, *Dendrium hugeri* and the pine-barren species *Dendrium buxifolium* were derived.

EDWARD W. BERRY.

JOHNS HOPKINS UNIVERSITY, BALTIMORE, MD.

[4] Hollick, *loc. cit.*, p. 230, pl. 71, fig. 9.

NOTES AND LITERATURE

HEREDITY

A Case of Non-Mendelian Heredity.—That hereditary characters which behave in accordance with Mendel's law of segregation depend in some way upon the chromosomes can hardly be questioned. Biologists, however, have been loath to believe that all hereditary characters are thus related to chromosomes. It is especially gratifying, therefore, to find completely worked out a type of inheritance which differs radically from the Mendelian type and which appears to be entirely cytoplasmic in character. The law of transmission in this case is of unusual interest. The case is reported by Dr. Erwin Baur, of Berlin.[1]

In this paper Dr. Baur describes several types of variegation. The first consists of variegation due to pathological conditions (auto-infection or auto-intoxication) and is not hereditary. By overcoming the auto-intoxication such plants are converted into ordinary green plants. On the other hand, ordinary plants can be infected with this condition by graft-symbiosis with an infected plant. This condition is not transmitted by seed. It is called by the author "infectious chlorosis," and is accompanied by a partial loss of green pigment in the chlorophyll grains. Several previous papers on this type of chlorosis by the author are referred to.

The second type of variegation consists of fully constant races whose chromatophores carry a diminished amount of green coloring matter, but the normal amount of yellow coloring matter. These races have distinctly yellowish-green leaves. In crosses with green races the yellowish green behaves as a Mendelian recessive.

The readers of this journal will remember that a similar character in tomatoes was reported recently by Professors Price and Drinkard, of the Virginia Experiment Station, and the character in this case behaved also as a Mendelian recessive.

[1] Erwin Baur. The Nature and Hereditary Relations of the Albo-Marginate Horticultural Variety of *Pelargonium zonale*. *Zeitsch. f. Abst.- u. Vererb.*, Bd. I, 1909, H. 4.

In another class of yellowish-green races, which are in a sense constant, the yellow-green plants are all heterozygote and Mendelize into one fourth clear yellow incapable of development, one fourth pure green, constant in later generations, and two fourths yellow-green, which splits again as above. This case was treated of by Dr. Baur in a former paper.[2]

Many other types of variegation exist. One of them is reported in the review of Professor Correns's paper below. The present paper of Dr. Baur's deals with another type of variegation, namely: white margined leaves, such as those found in varieties of *Acer negundo, Cornus alba, Pelargonium zonale* and numerous other species. The investigation was confined largely to the last-mentioned species. Little was previously known of the inheritance of this character. Several authorities had stated that such plants (with white margined leaves) produce only seedlings that are pure white and incapable of development.

Dr. Baur's studies show that the white margined plants of *P. zonale* are covered with two or three layers of cells containing colorless chromatophores which can not assimilate CO_2 but which can manufacture starch from sugar. The whole plant is covered by this white tissue. Near the leaf margin the two white layers form the whole of the tissue and thus give the peculiar marking on these leaves.

The line of demarcation between the white cells and ordinary cells is definite. One gets the impression that all the descendants of a white cell are white and all those of a green cell are green. This can not be definitely determined by microscopic study, but the experimental results reported below practically prove that such is the case.

Four white margined plants obtained from different sources all, when self-fertilized, produced only white seedlings, which soon died because they were incapable of assimilating CO_2. Some of these plants occasionally produced green branches which arose by the green tissue breaking through the superficial covering of white. Seed from these green branches produced normal green plants which propagated true to seed. On the other hand, white branches, when close fertilized, produced only white seedlings. (An occasional branch was pure white without the underlying green tissue.)

[2] *Ber. d. Den. Bot. Gesell.*, 25, 1907, p. 442, and *Zeitsch. f. Abst.- u. Ver.*, 1, 1908, p. 124.

Crosses made between flowers on pure white branches and other flowers on ordinary green plants gave thirty-nine green seedlings and seven green-white marbled plants. These crosses were made both ways, but only one seed, resulting in a green plant, was raised from the cross of green (♂) on white (♀).

Several crosses made both ways between white margined plants and ordinary green plants gave 199 pure green, 41 green-white marbled, and 4 pure white seedlings. Crosses between white margined and pure white branches gave all pure white seedlings. Evidently, white branches and white margined branches produce only white gametes, while green branches or green plants produce only green gametes.

Of the green-white marbled seedlings—that is, green and white spotted, some formed only white leaves and died when the spotted cotyledons ceased to function.

A second class formed only green leaves and became ordinary green plants when the spotted cotyledons dropped off. Their seedlings, about 50 in number, were all ordinary green plants.

A third class grew stems that were white on some sides and green on others. On such stems leaves attached to white surface were wholly white, and those attached to green surface were wholly green. Leaves attached on the line of union between green and white were correspondingly green and white. Branches which grew from the axils of the leaves behaved in exactly the same way as the leaves in regard to the green and white color.

These facts render it clear that the marbled seedling consists of two kinds of tissue—green and white. The descendants of white cells are white and those of green cells are green. A green and white seedling or branch may become either green or white by the growing point becoming overcapped by the one or the other kind of tissue. Of 23 marbled plants observed 20 became green and two white in this manner.

But the development of a marbled branch or plant may proceed in a different manner and one which clears up the difficulty concerning the nature and hereditary relations of the white marbled plants. In a marbled stem the line of contact between the two kinds of tissue may extend radially inward, or the white tissue may extend in a thin layer some distance over the green. A leaf rising centrally on a line of contact extending radially inward will be half white and half green; but a bud originating

from a part of the stem where the green tissue is covered by a thin layer of white is itself constituted of green tissue covered by white and produces ordinary white margined leaves. New albomarginate plants may thus be obtained from these marbled seedlings by taking branches which thus arise from parts of the stem where the white tissue forms a thin layer over the green. The white margined plants are thus to be regarded as "periclinal chimeras," while the marbled plants are "sectorial chimeras." White or green branches may arise from the white margined plants as the result of irregularity in cell division at the growing point.

The inheritance of the albomarginate character is now clear. In a white margined plant pollen and ovules are produced from white tissue only and hence carry only the white character. The seedlings are therefore white.

Sectorial chimeras were found in which the green tissue was superficial and the white central, thus giving leaves that were green on the margin and a paler color in the center, on account of the white tissue in the center of the leaf. One of the plants grown from a green branch occurring on an albomarginate plant was of this nature. Its seed produced only ordinary green plants.

The origin of the mosaic seedlings from a cross between white margined and green is not yet fully clear. Careful study of such of these seedlings as were recorded pure white revealed indications of green tissue in the hypocotyls. Likewise, those regarded as pure green revealed indications of white tissue. All of the seedlings from the green-white cross are probably mosaics, the differences being due to the fact that in some of them the white tissue, in others the green, is confined to a few cells, the remainder of the plant developing from the other tissue.

It is important to note that in some of these mosaics, or marbled plants, white "islands" may appear in several parts of the plant. These islands are evidently not derived one from the other. It can, therefore, be asserted that the differentiation of these white cells occurs more than once during the development of a plant and that the white cells must result from the division of cells that are green in appearance. (It is important to remember that green is dominant in the cross.) Just when these white cells arise can not be stated so positively. They may certainly arise after the formation of the cotyledons has begun.

The author offers the following tentative explanation of the origin of this white tissue in the crossbred green-white plants. The fertilized ovum contains both green and white chromatophores. In cell divisions of the embryo the chromatophores are distributed to the daughter cells more or less according to chance. If a cell receives only white chromatophores this cell will have only white descendants. If a cell receives only green chromatophores its descendants will be pure green cells. A cell receiving both kinds may later produce either pure white or pure green at any cell division. Should a cell which is later to develop into cotyledons and growing point receive only one kind of chromatophores, then the resulting seedling will appear to be only pure white or pure green, as the case may be. Since pure white cells may have only pure white descendants and pure green only pure green, while mixed cells may have three kinds of descendants, it naturally follows that after many cell divisions the percentage of mixed cells in the plant practically vanishes.

The above hypothesis makes only one assumption that is not demonstrated; that is, that the fertilized egg cell has two kinds of chromatophores, namely: white and green. According to current teaching the chromatophores are derived entirely from the egg cell; but, according to the author, this may well be considered not an established fact. If current teaching on this point is correct, then we have here a very remarkable case. It would then be necessary, according to Dr. Baur, to assume that in the cross, female white on male green, a part of the white chromatophores of the egg may become green under the influence of the male nucleus, and that in the reciprocal cross a part of the white chromatophores would have to become green under the influence of the male nucleus. Such a condition is thinkable, but no such case is known. Should it be proven, however, that the male sexual cell carries chromatophores, then the inheritance of the albomarginate character is fully explained.

These results of Dr. Baur's call for a detailed study of the chromatophores from one sexual cell stage to the next. The writer would suggest another possible explanation of the phenomena discussed above. The male nucleus may bring with it into the cell something which is not a part of the nucleus itself but is cytoplasmic in its nature. This may develop and give rise to a part of the cytoplasm of the fertilized egg. Then something in the chemical constitution of this cytoplasm causes the chro-

matophores which develop in it to lose their power of assimilating CO_2. Subsequent cell division would occasionally throw off cells of pure white, which would give rise to the white tissue. This is only suggested as a mere possibility. That the condition can hardly be caused by the male nucleus itself would seem to be indicated by the fact that descendants of this nucleus must be present in those cells which are pure green. If the white character were carried by the chromosomes, then it would appear that all the green cells would necessarily be affected. There seems to be no question that the white character is cytoplasmic in its nature, and this would account for the fact that it does not follow Mendel's law of segregation in the reduction division. The segregation, in fact, occurs in somatic divisions.

Professor Correns reports another interesting study of variegation in a recent article,[3] of which the following is a summary.

Plants deficient in chlorophyll have hitherto been called "aureas." The author now restricts this term to plants which are deficient in chlorophyll but which have the normal amount of yellow-color materials, zanthophyll and carotin. Those deficient in all three are termed "chlorinas." Those of the latter type obtained in commerce were found to be dwarf as compared with normal sorts. The leaves and flowers are also relatively smaller. This smaller size is shown to be partly a consequence of deficiency in chlorophyll and the consequent insufficient nourishment of the plant. On the other hand, it is partly due to a specific Mendelian character of dwarfness, and the Mendelian dwarf habit is strictly correlated with small leaves and small flowers.

The chlorina races are fully constant. Variegated races have spots of green on leaves otherwise of chlorina type. In some cases these spots vary in number and size from leaf to leaf; in others they are hereditarily fixed. Some of the variegated races, on account of the smallness of the green spots, are difficult to distinguish from the chlorina types. On some of the variegated plants, especially those having much green, typical green branches occur, and this phenomenon is characteristic of the plants on which it occurs. That is, the same plant year after year produces these green branches. Every possible gradation

[3] Investigations on Inheritance of Yellowish Green and Variegated Races of *Mirabilis Jalapa*, *Urtica pilulifera* and *Lunaria annua*. *Zeitsch. f. Abst.- u. Vererb.*, 1, 1909, H. 4.

exists between a small green fleck on a leaf and a typical green branch.

The variegated types do not reproduce strictly true to seed. They sometimes throw green plants. These green plants do not simply represent extremes of variation because they are too numerous and offer a secondary maximum in the curve of distribution. On the other hand, variegated plants have thus far not produced any of the pure chlorina type. Some of the pure green reversions produced progeny all of which are green. A larger number gave some variegated and some green, the green nearly always predominating in the progeny. The thus obtained variegated plants gave some normal green progeny, and the normal greens thus obtained gave only occasionally all normal greens. A green branch on a variegated plant, when self fertilized, gave three variegated and four green plants. It was not possible to explain variegation in these species as a cross between the chlorina and the normal green types. In the cross between chlorina and typica (normal greens) the latter is dominant, but not absolutely so. The chlorophyll content of the hybrids is about 90 per cent. of that in the normal greens. In some cases in the second generation of this cross, the hybrids split into chlorinas and greens in perfect Mendelian fashion. In others variegated plants occur in the second generation; the reason for this is given below.

Dwarf and normal stature behave as a pair of Mendelian characters independent of leaf color, the dwarf habit being recessive. Generally speaking, chlorina plants not dwarf were not quite so tall as the normal greens because of their inability to manufacture starch at normal rate. The tall chlorinas and the dwarf greens produced from this cross were new types, the latter being especially attractive.

In the cross variegata on typica the latter is dominant and segregation occurred in Mendelian fashion. On account of the variability of the variegated type (this type produced some greens) the per cent. of greens in F_2 was somewhat in excess of 75 per cent. Here again the semi-dwarf and normal stature acted as a pair. In the cross between chlorina and variegata the latter proved to be dominant. Normal splitting occurred in the second generation. As in other cases, a few greens arose from the variegated plants. The medium stature of the variegated plants behaved as a pair with the dwarf stature of the chlorina plants.

In each of three experiments the cross variegata on typica gave chlorinas, variegated plants and normal greens in the ratio 1:3:12. The plants used in these crosses were known to be constant. In one experiment a cross between typica and chlorina gave in F_2 63 green, 4 variegated and 3 chlorinas. Here also the chlorina form was known to be constant. This unusual behavior is explained by Professor Correns in the following manner:

The occurrence of normal greens amongst the progeny of variegata is due to the revival of a latent factor for green (G). The color factors present in the various types are assumed to be

G = presence; g = absence (or latency) of green factor.
V = presence; v = absence (or latency) of variegata factor.
C = presence; c = absence (or latency) of chlorina factor.
V is epistatic to C.
G is epistatic to V and C.
Variegated races have the formula gVC (or gVc).
Chlorina races have the formula gvC.
Normal green races have the formula GVC (or GvC, or GVc, or Gvc).

The cross between green and variegata thus becomes:

GVC + gVC, in which F_2 = 3 green to 1 variegated; or
GvC + gvC, in which F_2 = 12 green, 3 V and 1 C.

The cross green on chlorina becomes:

GvC + gvC, in which F_2 = 3 green to 1 chlorina; or
GVC + gvC, in which F_2 = 12 green, 3 V and 1 C.

The cross variegated on chlorina becomes:

gVC + gvC, in which F_2 = 3 V + 1 C.

The cross between the very distinct species *Mirabilis Jalapa variegata* and *M. longifolia* typica give hybrids that are quite alike in F_1, but highly variable in F_2. Yet all the characters involved appear to "Mendelize." For instance: green and variegated leaves, normal and dwarf stature, erect and trailing habit form Mendelian characters.

In contradistinction to the white margined *P. zonale* studied by Baur, a white margined form of *Lunaria annua* studied by Professor Correns reproduced true to seed, and when crossed with a green leafed form the margin behaved as a recessive Mendelian character.

A recent article by Whitney in the *Journal of Experimental Zoology*[4] is of interest in connection with the type of heredity

found by Baur in *P. zonale*, as it bears upon the relation of plastids in the cytoplasm to heredity. Eggs of *Hydatina senta* were subjected to centrifugal force, which separated the contents into three layers, described as a pink zone, a middle clear zone and a gray zone. The first cleavage plane was variously arranged with reference to these zones in different eggs, yet the eggs developed into normal adults which produced normal young. This would seem to indicate that the plastids in the pink and the gray zones have little to do with differentiation in development. This does not prove, however, that other plastids might not have such influence.

Professor Vernon L. Kellogg, of Leland Stanford University, has recently published an important paper on inheritance in silk worms.[5] In common with Coutagne and Toyama he found many Mendelian characters in these insects. This was especially the case for characters of the larvæ. For instance, the mouricaud pattern (a dark form) in the larvæ was dominant to white. The same was true of the tiger banded, or zebra, type of coloring. A white type with a well marked darker pattern, which in the laboratory is known as "the patterned type" behaved usually as a unit character recessive to zebra and dominant to white. Its behavior was entirely Mendelian in crosses with white, but there was some irregularity in crosses with zebra. The irregularities mentioned by Professor Kellogg are fully explained by assuming that the pattern character and the zebra character are independent Mendelian characters, and that when both are present in the same individual they can both be discerned.

The author was puzzled a good deal by the behavior of white and attributes the fact that it was sometimes dominant and sometimes recessive to individual or strain idiosynerasies. A large number of matings are given with their results in the first and second generation to illustrate the idiosynerasies relating to inheritance of white. Evidently, Professor Kellogg was dealing with animals in which there are two distinct types of white, one dominant and the other recessive. A similar case has been well made out for poultry, and I have found indications of two such white characters in swine, though the recessive white in swine is not fully made out. All of the irregularities in the inheritance

[4] D. D. Whitney. Effect of a Centrifugal Force upon Development and Sex. *Journ. of Exp. Zool.*, VI, No. 1, January, 1909.

[5] Leland Stanford University Publications, University Series No. 1.

of white found by Professor Kellogg fall immediately into line with Mendelian principles by the assumption of these two types of white, which are sometimes found in the same individual.

Some of the most interesting work reported by Kellogg relates to cocoon coloring. He found one type of salmon colored cocoon which when crossed with either the dominant or the recessive white behaved as a Mendelian unit and broke up into every shade from very pale salmon to golden yellow. This is an interesting case of a variable Mendelian character. Generally speaking, the various cocoon colors were Mendelian units, the only irregularity being the marked variation of some of the colors after hybridization. Wing pattern in the adults and the color and adhesiveness of the eggs showed no Mendelian differences. Apparently the variations which occur in these characters are due to the fluctuations of a single Mendelian character, and hence no pairs are formed.

The effect of insufficient nutrition on the dominance of characters was studied, the results being entirely negative. Kellogg attributes the Mendelian nature of the larval color characters to their origin by mutation, while the fluctuating variability of cocoon characters are supposed to be due to their origin by selection of fluctuating characters. As pointed out by the writer elsewhere, the manner of origin of a character, whether by gradual modification or by sudden change, has no relation to its Mendelian behavior, so that the fact that certain characters behave as Mendelian characters is in no way an indication that they are mutations.

Certain characters which fluctuated widely, and in which no indication of Mendelian inheritance was found, were amount and quality of silk in the cocoon, wing pattern, wing venation, certain larval markings, degree of adhesiveness in eggs and the number of broods produced in a season. These characters present very interesting objects of study, and it is gratifying to learn that Professor Kellogg is giving them further attention. Coutagne is quoted to the effect that selection for ten years had no effect on the richness of silk. This is important in its relation to the effect of selection on fluctuating characters.

One of the races on which these studies were made lays eggs which are non-adhesive. When crossed with races laying adhesive eggs, the non-adhesiveness disappears and does not reappear even in the second generation ordinarily. This suggests

that non-adhesiveness is due to the latency of a character which is revived under the stimulus of hybridization. It is stated that wing pattern does not seem to be capable of any considerable modification by even a most careful and persistent selection. This is in line with all recent work on selection in fluctuating characters when the effect of hybridization has been eliminated.

Variations of wing venation are of special interest. They seldom took the form of additions to the system of veins, and when they did the modifications were only slight. Generally, these variations consisted of the loss of veins in part or in whole. In many cases veins became reduced to tracheæ without chitinous covering. In a few cases tracheæ appeared in what may be supposed to be the position of ancient veins, thus representing partial restorations of lost characters. Many sports occurred in wing pattern. Generally speaking, these were not hereditary. Melanism occurring as a sport showed a slight tendency to be inherited, and further studies of this matter are in progress. Occasional moths with power of flight and less frequently appearing individuals with rudimentary wings showed no tendency to transmit these characters.

Some of the most interesting features of Professor Kellogg's work are the marked fluctuations of characters whose stages can not be fixed by selection. Yet the fact that certain of the races were constant with respect to a particular stage of such a character, as, for instance, the Italian salmon with reference to cocoon color, which on hybridization breaks up and becomes highly fluctuating, is of great interest. The question whether fluctuations can be fixed by selections is as yet debatable. The Italian salmon seems to be such a fixed stage. On the other hand, some of Professor Kellogg's results indicate that the Italian salmon may be a compound character, a fact which might account for its variability. Perhaps long continued selection might, after a while, fix such characters, especially when the fluctuations cover such a wide range. The writer hardly agrees with the assumption that such characters are non-Mendelian. It would seem rather that their stages are simply not stable from generation to generation. If they could be fixed by selection or otherwise one might then expect the fixed stages to behave toward each other as Mendelian pairs.

Dr. East reports some interesting studies on inheritance in

sweet corn.[6] He points out that Correns has shown that the peculiarity of sweet corn is due simply to inability to complete the formation of normal maize starch. The presence and absence of this starch forming ability behaves as an ordinary Mendelian pair. The absence of the ability to form starch is the one character peculiar to the sweet corn group. It is shown that the sweet corn may be either of the dent or the flint type in potential hereditary characters, and suggests that the early history of sweet corn indicates that it arose amongst the flints and spread to the dents by hybridization. Dent corns tend to have from 12 to 28 rows; flints usually have 8 and may have 12 rows as the mode. Dents are little given to tillering, while tillering is characteristic of flints. Flint varieties are also characterized by large bracts at the end of the husks, dents by small bracts or none. Sweet corn, on the other hand, runs the whole gamut of the above characters. For instance, Stowell's Evergreen is a dent, having 16 to 24 rows. Golden Bantam and Black Mexican are flints.

When the starch forming character is introduced into sweet varieties from either dent or flint sources the dent or flint character of the sweet parent becomes evident. The author thinks that the dent or flint character appearing in sweet corn is determined largely, but possibly not entirely, by the character possessed by the female parent.

W. J. SPILLMAN.

[6] E. M. East. A Note Concerning Inheritance of Sweet Corn. *Science*, N. S., XXIX, No. 742.

The Study of Stellar Evolution

An Account of Some Modern Methods of Astrophysical Research

By GEORGE ELLERY HALE

The introduction of photographic methods, the improvement of telescopes, and the rapidly increasing appreciation of the value to astronomy of physical instruments and processes, have revolutionized the observatory. From a simple observing station it has been transformed into a great physical laboratory, where images of the sun and stars are studied with many powerful instruments, and celestial phenomena are experimentally imitated with the aid of electric furnaces and other sources of intense heat. The result has been a great gain in our knowledge of the origin, development, and decay of stars. This books explains in a popular way how the life histories of the sun and stars are investigated. One hundred and four half-tone plates, made from the best astronomical negatives, place before the reader the most recent results of celestial photography in most of its phases.

250 pages, 104 plates, 8vo, cloth; net $4.00, postpaid $4.27

Address Dept. 62

THE UNIVERSITY OF CHICAGO PRESS

CHICAGO **NEW YORK**

Published in Europe by William Wesley and Son, 28 Essex Street, Strand, London, Price, 16s. 6d.

ESSAYS PHILOSOPHICAL AND PSYCHOLOGICAL.

IN HONOR OF WILLIAM JAMES, PROFESSOR IN HARVARD UNIVERSITY BY HIS COLLEAGUES AT COLUMBIA UNIVERSITY

This volume is intended to mark in some degree its authors' sense of Professor James's memorable services in philosophy and psychology, the vitality he has added to those studies, and the encouragement that has flowed from him to colleagues without number. From Prefatory Note.

PHILOSOPHICAL ESSAYS.

The New Realism.....GEORGE STUART FULLERTON
Does Reality possess Practical Character?.....JOHN DEWEY
A Factor in the Genesis of Idealism.....WENDELL T. BUSH
Consciousness a Form of Energy.....WM. PEPPERRELL MONTAGUE
Perception and Epistemology.....FREDERICK J. E. WOODBRIDGE
Substitutionalism.....C. A. STRONG
World-Pictures.....WALTER BOUGHTON PITKIN
Naïve Realism: What Is It?.....DICKINSON S. MILLER
Kant and the English Platonists.....ARTHUR O. LOVEJOY
A Critique of Kant's Ethics.....FELIX ADLER
The Abuse of Abstraction in Ethics.....HERBERT GARDINER LORD
Purposive Consistency, the Outline of a Classification of Values.....G. A. TAWNEY
The Problem of Method in Mathematics and Philosophy.....HAROLD CHAPMAN BROWN

PSYCHOLOGICAL ESSAYS.

Pragmatism in Æsthetics.....KATE GORDON
The Consciousness of Relation.....R. S. WOODWORTH
On the Variability of Individual Judgment.....FREDERIC LYMAN WELLS
The Validity of Judgments of Character.....NAOMI NORSWORTHY
Reactions and Perceptions.....JAMES MCKEEN CATTELL
A Pragmatic Substitute for Free Will.....EDWARD L. THORNDIKE

With Photograph of PROFESSOR JAMES.

LONGMANS, GREEN & COMPANY. **91 Fifth Avenue, New York City**

The American Naturalist

A Monthly Journal, established in 1867, Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Organic Evolution and Heredity

CONTENTS OF THE JANUARY NUMBER

Juvenile Kelps and the Recapitulation Theory. Professor ROBERT F. GRIGGS.

The Larva and Spat of the Canadian Oyster, Dr. J. STAFFORD.

Shorter Articles and Correspondence: Some Notes on the Traditions of the Natives of Northeastern Siberia about the Mammoth, WALDEMAR JOCHELSON. Age of Trotting Horse Sires, F. R. MARSHALL. The Occurrence of *Batrachoceps attenuatus* and *Autodax lugubris* in Southern California, WILLIAM A. HILTON.

Notes and Literature: *Experimental Evolution*—The Effect of the Environment upon Animals, Dr. FRANK E. LUTZ. *Experimental Zoology*—The Influence of the Size of the Egg and Temperature on the Growth of the Frog, SERGIUS MORGULIS. *Parasitology*—Cestodes of Birds, Professor HENRY B. WARD.

CONTENTS OF THE FEBRUARY NUMBER

Charles Darwin and the Mutation Theory. CHARLES F. COX.

Juvenile Kelps and the Recapitulation Theory. II. Professor ROBERT F. GRIGGS.

Notes and Literature: *Plant Phylogeny*—The Origin of the Archegoniates, Dr. BRADLEY M. DAVIS. *Holothurians*—Clark's The Apodous Holothurians, W. K. FISHER. *Lepidoptera*—The Blue Butterflies of the Genus Celastrina, Professor T. D. A. COCKERELL. *Vertebrate Paleontology*—The Lysorophidæ; Stegocephala; The Cotylosauria; The Oldest Known Reptile; The Age of the Gaskohle; Bison Occidentalis; Nectosaurus; Callibrachion, Dr. ROY L. MOODIE. *Parasitology*—The Sleeping Sickness Bureau, Professor HENRY B. WARD. *Exploration*—Camp-fires on Desert and Lava, Dr. ROY L. MOODIE.

CONTENTS OF MARCH NUMBER

Invitation Papers at the Baltimore Meeting of the Botanical Society of America; Darwin Memorial Session:—
Darwin as a Naturalist; Darwin's Work on Cross Pollination in Plants. Professor WILLIAM TRELEASE.
Darwin's Influence upon Plant Geography and Ecology. Professor FREDERIC E. CLEMENTS.
Darwin's Work on Movement in Plants. Professor HERBERT MAULE RICHARDS.

An Examination of Darwin's "Origin of Species" in the Light of Recent Observations and Experiments. Professor EDWIN LINTON.

The Distinction between Development and Heredity in Inbreeding. Dr. EDWARD M. EAST.

Breeding Experiments with Rats. Professor T. H. MORGAN.

Shorter Articles and Discussion: The Chub and the Texas Horn Fly, Dr. ROY L. MOODIE. A New Camel from the Lower Miocene of Nebraska, HAROLD JAMES COOK.

Notes and Literature: *Heredity*—The Chondriosomes as Bearers of the Hereditary Qualities, F. PAYNE. Cultural Bed Mutations in the Potato.

CONTENTS OF THE APRIL NUMBER

Heredity of Hair Color in Man. GERTRUDE C. DAVENPORT and CHARLES C. DAVENPORT.

A Mechanism for Organic Correlation. Professor G. H. PARKER.

Recent Advances in the Study of Vascular Anatomy.
Vascular Anatomy and the Reproductive Structures. Professor JOHN M. COULTER.
The Progress of Plant Anatomy During the Last Decade. Professor EDWARD C. JEFFREY.

Shorter Articles and Correspondence: A Note on the Degree of Accuracy of the Biometric Constants, Dr. RAYMOND PEARL. Pure Strains as Artifacts of Breeding. O. F. COOK.

Notes and Literature: *Heredity*—The Nature of "Unit" Characters, Dr. W. J. SPILLMAN. *Environment*—Dr. FRANK E. LUTZ. *Experimental Zoology*—Hybridology and Gynandromorphism, Professor T. H. MORGAN. *Echinodermata*—Red Sea Crinoids, Dr. AUSTIN HOBART CLARK.

CONTENTS OF THE MAY NUMBER

The Categories of Variation. Professor S. J. HOLMES.

The General Entomological Ecology of the Indian Corn Plant. S. A. FORBES.

Notes and Literature: *Biometrics*—Some Recent Studies on Growth. Dr. RAYMOND PEARL. *Experimental Zoology*—Cuénot on the Honey Bee, Professor T. H. MORGAN. *The Upholding of Darwin*—Poulton and Plate on Evolution, V. L. K.

CONTENTS OF THE JUNE NUMBER

Heredity and Variation in the Simplest Organisms. Professor H. S. JENNINGS.

The Color Sense of the Honey Bee—Is Conspicuousness an Advantage to Flowers? JOHN H. LOVELL.

Variation in the Number of Seeds per Pod in the Broom, Cytisus scoparius. Doctor J. ARTHUR HARRIS.

Present Problems in Plant Ecology:
The Trend of Ecological Philosophy. Professor HENRY C. COWLES.
The Present Problems of Physiological Plant Ecology. Dr. BURTON LIVINGSTON.

Notes and Literature: Notes on Evolution, V. L. K. DeVries's Species and Varieties, Dr. GEORGE H. SHULL. *Embryology*—On the Totipotence of the First Two Blastomeres of the Frog's Egg. Dr. J. F. MCCLENDON.

Single Number 35 Cents **Yearly Subscription, $4.00**

The NATURALIST will be sent to new subscribers for four months for One Dollar

THE SCIENCE PRESS

Garrison, N. Y. **Sub-Station 84: NEW YORK** **Lancaster, Pa.**

VOL. XLIII, NO. 512 AUGUST, 1909

THE AMERICAN NATURALIST

A MONTHLY JOURNAL
Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

CONTENTS

Page

I. The New Flora of Krakatau. Professor DOUGLAS HOUGHTON CAMPBELL . 449

II. A Male Crayfish with Some Female Organs. Professor E. A. ANDREWS . 461

III. Present Problems in Plant Ecology:
Problems of Local Distribution on Arid Regions. Professor VOLNEY M. SPALDING 472
The Relation of the Climatic Factors to Vegetation. Professor EDGAR N. TRANSEAU 487

IV. Notes and Literature: Recent Experiments on the Inheritance of Coat Colors in Mice, PROFESSOR T. H. MORGAN. Some Experiments in Breeding Slugs, PROFESSOR T. D. A. COCKERELL. 494

THE SCIENCE PRESS

LANCASTER, PA. GARRISON, N. Y.

NEW YORK: SUB-STATION 84

The American Naturalist

MSS intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS

Lancaster, Pa. Garrison, N. Y.

NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

Important New Scientific Books

PUBLISHED BY THE MACMILLAN COMPANY

Botany

The Origin of a Land Flora. A Theory based upon the facts of Alternation. By F. O. BOWER, Sc.D., F.R.S. With numerous illustrations.

Cloth, gilt top, xi+727 pp., illus., index, 8vo, $5.50 net.

NOTE.—A profound study in the morphology of the lowest forms of plants, with special reference to the development of their reproductive systems. The author endeavors to show that the present land flora has originated from an aquatic ancestor, and traces the methods of specialization to the land habit, and the establishment of the forms of the higher plants. A book of the highest importance not only to botanists but to biologists in general.

NEW AND STANDARD HAND-BOOKS ON AGRICULTURE, ETC.

Elements of Agriculture, Southern and Western. By W. C. WELBORN, B.S., M.S., M.P.A.

Cloth, xvi+329 pp., illus., appendix, glossary, index, 12mo, $.75 net.

NOTE.—This is a thoroughly modern treatise on farming as practiced in the Gulf States, from the point of view of the scientific agriculturist. It is adapted to school use, but is of practical service to any farmer in that part of the country. The author is vice-director of the Texas Experiment Station.

Re-issues of the highly valued Hand-Books known as the Garden Craft and Rural Science Series, edited by L. H. BAILEY, of Cornell University, Editor of "Cyclopedia of American Horticulture," "Cyclopedia of American Agriculture," etc.

The Principles of Fruit Growing. By L. H. BAILEY.
Tenth Edition, $1.50 net, by mail $1.66.

Irrigation and Drainage. By F. H. KING.
Fifth Edition, $1.50 net, by mail $1.68.

Principles of Vegetable Gardening. By L. H. BAILEY.
Sixth Edition, $1.50 net, by mail $1.68.

Bush Fruits. By FRED W. CARD.
Fourth Edition, $1.50 net, by mail $1.66.

Fertilizers. By EDWARD B. VOORHEES.
Tenth Edition, $1.25 net, by mail $1.38

Farm Poultry. By GEO. C. WATSON.
Sixth Edition, $1.25 net, by mail $1.42

Published By **The Macmillan Company** 64-66 5th Ave., New York

THE
AMERICAN NATURALIST

VOL. XLIII *August, 1909* No. 512

THE NEW FLORA OF KRAKATAU

PROFESSOR DOUGLAS HOUGHTON CAMPBELL

STANFORD UNIVERSITY

IN August, 1883, there occurred in the Straits of Sunda, between Java and Sumatra, the most violent volcanic eruption of which there is any record. This catastrophe involved the island of Krakatau (Krakatoa, as it is usually written in English), as well as the two small neighboring islands, Verlaten and Lang Island. As a result of this eruption about two thirds of the larger island, which was nine kilometers long and five in width, disappeared, while the other islands were noticeably increased in size, and the whole floor of the ocean in the vicinity was completely changed. It was estimated that the total amount of matter ejected during the successive eruptions from May to August amounted to eighteen cubic kilometers, and this immense mass of stones, ashes and volcanic dust was scattered over an enormous area, the ashes being carried many hundred miles, and life of all kinds upon the islands was completely annihilated. Many will recall the brilliant crimson sunset skies that were observed all over the world some months later. These were caused by the presence of fine volcanic dust from Krakatau which, suspended in the upper atmosphere, was carried entirely around the world. The detonations from the explosions were said to have been heard nearly three thousand miles away; and at Buiten-

zorg and Batavia, in Java, about 150 kilometers away, the explosions were likened to the discharge of cannon near at hand, and were so violent as to shake the houses to such an extent that objects were thrown down.

The effect of the great mass of hot ashes and pumice that completely covered the islands, was to entirely destroy every vestige of the luxuriant vegetation which before the eruption clothed the island of Krakatau with a dense forest extending from the shore to the summit of the highest peak, *Rakata*, 832 meters in height.

The island of Krakatau, therefore, after the eruption, was very efficiently sterilized, and offered a most unusual opportunity for studying the establishment of the vegetation upon a large area absolutely barren and comparatively isolated. The nearest land is an island some nineteen kilometers distant on which the vegetation was also largely destroyed, while the large islands of Java and Sumatra are respectively 35 and 45 kilometers distant.

Fortunately there was a man who fully appreciated the importance of this unique opportunity, and determined to trace the reestablishment of the new flora upon the desolated island. The botanical world owes a great debt to Professor Treub, the distinguished botanist who has done so much to advance the study of botany in the tropics, both by his own important investigations and by the building up of the unrivaled facilities for research offered by the magnificent gardens and experiment stations in Java.

Treub's visit was made in 1886, three years after the eruption, and subsequently the island was again visited by him in 1897, and a third expedition was made in 1905.

In the spring of 1906, while engaged in botanical study at the mountain station Tjibodas, in Java, I received word that a visit to Krakatau was being arranged for, and was invited to join it. The results of this trip have been presented in admirable fashion by Professor A.

Ernst,[1] of the University of Zürich, to whose efforts and energy the successful results of this trip were largely due. Considering the very brief time at our disposal, the amount of material secured by Professor Ernst and the completeness with which it was worked out were really remarkable.

On the morning of April 24 our little party set sail from Tandjong Priok, the harbor of Batavia, for our brief cruise among the islands of the Straits of Sunda, for Krakatau. The little coasting steamer "Snip" (Snipe), which had been placed at our disposal for the trip, proved most comfortable, and her captain did everything possible to make our trip a pleasant one. The party included, besides Professor Ernst, Mr. C. A. Backer, of the Buitenzorg Gardens, whose intimate acquaintance with the Malaysian flora was very much appreciated, and Dr. A. A. Pulle, of the University of Utrecht, who, like myself, was working at Buitenzorg. The weather proved all that could be asked, and the voyage over the calm, dazzling blue sea among the picturesque islands was one long to be remembered. As we sailed out of the harbor we could see in the distance the great volcanoes Salak and Gedeh, which dominate Buitenzorg, and which had become quite like old friends. On the slopes of Gedeh lies the mountain station Tjibodas, where I had spent several happy weeks, and to which I was going back on my return from Krakatau. Opportunity was given us to stop at several points *en route*, one being Vlakke Hoek, the southernmost point of the westerly peninsula of Sumatra. All of the places where we stopped showed a most interesting strand flora, including many striking plants, some of which we encountered again on the shores of Krakatau. The shallow lagoons within the coral reefs of these islands were full of interesting things, corals, sea anemones, gorgeously

[1] "The New Flora of the Volcanic Island of Krakatau." By A. Ernst, Ph.D., professor of botany in the University of Zürich. Translated by A. C. Seward, F.R.S., professor of botany in the University of Cambridge. **Cambridge, at the University Press, 1908.**

colored fish and many interesting algæ. Professor Ernst collected a large number of striking siphoneous algæ which abound among the coral reefs. (For a list of the plants collected at these intermediate stations, see Professor Ernst's Memoir, pages 9 to 18.)

Vlakke Hoek was devastated by the great waves resulting from the eruption of Krakatau, the waves reaching a depth of fifteen meters and sweeping away practically everything except the great iron light house tower, which alone remains of buildings existing before the eruption.

From Vlakke Hoek we crossed the Straits of Sunda to the southwest coast of Java (Java's first point), and *en route* had our first view of the peak of Krakatau rising above the clouds to the east. The bold shores of the Javanese coast presented a great contrast to the flat, monotonous shore at Vlakke Hoek in Sumatra. The difference in the topography of the land is reflected in the plants, which were strikingly different from those of Vlakke Hoek (see Ernst, pages 24 to 26). Early in the morning of April 26, we approached the Krakatau group of islands.

The view of the island of Krakatau from the north is most impressive. During the great eruption the volcanic peak Rakata was cleft down the middle, so that from peak to base its northern side presents a perpendicular cliff half a mile high, falling sheer into the sea, which at the foot of the cliff is now more than three hundred meters deep. The exposed face of the cliff forms a perfect median section of the cone, and the arrangement of the rocks of which it is built up offers a most extraordinary picture. Professor Ernst took some admirable photographs, which are reproduced in Plate III of his Memoir.

At six o'clock we dropped anchor and soon after were taken ashore in one of the ship's boats. The landing was made on the east side of the island where the outer part of the beach forms a broad zone of mingled pumice, coral and all sorts of débris; fragments of driftwood, seaweed

and a conglomeration of seeds and fruits washed up by the tide. Many of the fruits washed upon the shore were those of characteristic strand plants like cocoanuts, screw pines, Nipa palms and others. Most of these show various devices for facilitating their transport by water, and some of them had germinated and were trying to get a foothold in the loose mass of pumice and coral sand.

Above this outer drift zone there is a characteristic sandy belt where various typical strand plants have established themselves. The long prostrate stems of *Ipomœa pes-capræ*, that most ubiquitous of tropical strand plants, sprawled over the sand, and with these were masses of the curious grass, Spinifex, and a yellow flowered leguminous plant *Vigna lutea*, a euphorbia with thick, waxy leaves, and various other species common to the outer littoral zone of the Indo-malaysian region. While fruits of the Nipa palm were found, the plant has not yet got a foothold in Krakatau, and there is as yet no mangrove formation established.

Back of the beach a thrifty belt of forest is conspicuous and could be plainly seen long before we reached the island. Some of the trees in this forest are at least fifty feet high, the tallest being specimens of the curious *Casuarina equisetifolia* Forst., a genus mainly confined to the Australasian region, but with a few species widely distributed throughout the Malayan Archipelago. Associated with these were found specimens of screw pines (Pandanus sp.), and the striking *Terminalia Catappa* L., whose whorled branches and great shining leaves make it one of the most notable of tropical trees. Perhaps the most beautiful of all the trees of this strand forest is *Barringtonia speciosa* Forst., a tree with large, glossy, dark green leaves and great white flowers with a crown of stamens looking like an enormous myrtle flower. The curious four-sided angular fruits of this tree are very common along the beach. Of the few climbing plants the most conspicuous was *Vitis trifolia* L.

After spending some time exploring the beach and

strand forest, we pushed inland toward the south, not without much exertion and perspiration. The unclouded rays of an equatorial sun beat down pitilessly upon us, and when, after struggling over blocks of pumice and through thickets of tall grasses and bushes, we finally reached a small grove of cocoanut palms, full of fruit, we threw ourselves down on the ground under their grateful shade and took a well-earned rest. No time was lost in sending one of the natives up into a tree for green nuts, which were thrown down and quickly opened, and never did anything taste better than the cool, sparkling cocoanut water after our exhausting march through the fierce heat of the jungle.

From the ship we had seen that the ravines on the flank of the Rakata were filled with a dense growth of trees, forming the beginning of a new forest, but it was quite impossible to guess what the trees were. We tried to cross the open tract lying between the belt of forest on the shore and the cone in the center of the island, but we had to give up the attempt after penetrating some distance inland, following the dry bed of a stream for part of the way. The land was terribly rough and covered in many places with a dense jungle of grasses ten or fifteen feet high, through which he had to hew a path with the wicked-looking cutlasses which every Malay carries when traveling. The way lay over steep ridges, which grew worse and worse as we approached the cone, and finally we realized that with the short time at our disposal, and the limited means of cutting our way through the jungle and scrub, we should have to give up the attempt, which we did very reluctantly, and retraced our steps to the shore, where we embarked for the ship.

The monotony of the journey over the grass steppes in the interior of the island was broken by encounters with countless ants which built their nests everywhere, in the crevices of the rocks, among the roots of the grasses and shrubs, and even hanging from the branches of the shrubs and trees; and as we scrambled up the steep slopes

of the frequent small ravines, down would come showers of ants, swarming all over us but not doing any serious damage. Few showy flowers were seen, the most striking being several terrestrial orchids, one of which *Arundina speciosa* Bl. was quite common and decidedly handsome.

After boarding the ship, we sat sail for the north side of the island, where a landing was made at the base of the rock wall formed by the fractured face of the riven cone of Rakata. As we approached the face of the cliff, we were startled to see what looked like puffs of smoke rising from various fissures in the cliff. Remembering the history of the mountain, and also having just received the news of the eruption of Vesuvius and the terrible earthquake at home, the thought occurred that perhaps Krakatau was getting ready for another outburst, which to say the least, was not reassuring. But we finally discovered that the "smoke" was merely clouds of dust caused by the falling of débris from the face of the cliff.

Our landing was made in a broad bay where there is a narrow beach, but the development of the strand flora is much less advanced than on the south side of the island. Ferns were noticeably abundant, as they were on the other parts of the island when it was first visited after the eruption. *Nephrolepis exaltata* Schott was especially frequent, and in the crevices in the rocks we found numerous prothallia and young plants of a species of Gymnogramme and of several other ferns. Some of the ferns and other plants which were growing upon the ground here are usually epiphytes. Of these *Polypodium quercifolium* L. was the most conspicuous.

After exploring the interior and strip of land at the base of the cone, we returned to the ship. Before the sun went down we set sail for Java and soon the peak of Krakatau was left behind us. The next morning found us safely back in Tandjong Priok.

The Reestablishment of the Flora on Krakatau

When the island was first visited by a geological expedition two months after the eruption, the whole surface was buried under a layer of ashes and pumice averaging thirty meters in depth, and in some places as much as sixty meters. Thus, of course, every trace of life must have been quite annihilated and the sterilization was complete. An analysis of the ashes showed that, except for phosphorus and nitrogen, all of the elements necessary for plant life were present. (See Ernst, p. 50.) Ernst suggests that the other elements necessary for the establishment of a new flora were conveyed from the mainland in the form of dust, and that as a result of the intense electrical activity which accompanies the almost daily rains of the equatorial region, the atmospheric nitrogen is oxidized into the nitric and nitrous acids which furnish the necessary nitrogen. This with the salts and traces of organic matter in the ashes would have been sufficient in a very short time to allow the establishment of the first micro-organisms upon the island.

The first botanical expedition, as already stated, was made under the direction of Professor Treub in 1886, three years after the eruption. During this interval a considerable number of plants had already established themselves upon the island. The most important fact brought out by this trip was the great importance of the blue-green algæ in the early establishment of the new vegetation. Thin blackish, slimy films, formed by a number of species of Oscillatoria and other blue-green forms, were found in great quantity coating the surface of the ashes, and the gelatinous matrix of these low plants offered a substratum which was favorable for the germination of the spores of ferns and even for the seeds of a few phanerogams. It was found that the colonization of the island was quite as marked in the interior and upon the high cone as it was along the shore, but the plants of the interior of the island were for the most part

quite different. A remarkable fact was the great preponderance of ferns in the new flora. In the period of three years no less than eleven species had established themselves and formed the predominant feature of the new vegetation. In our visit to the north side of the island, where the reestablishment of the vegetation, as we have seen, was less advanced than on the south side, this preponderance of ferns was very marked, whereas in the other parts of the island they have been to a very great part supplanted by the phanogamous immigrants and several species seem to have disappeared. In the drift zone of the beach Treub found nine species of seedling plants, and in the central part of the island eight, two of which were the same as those upon the shore. Of the remaining six, four were composites and two grasses, all forms which would be distributed readily by the wind. These phanerogams, however, were far less numerous as individuals than were the ferns.

A series of visits to the islands was projected by Treub, but unfortunately the plan could not be carried out. and it was not until 1897 that a second expedition visited Krakatau. This second expedition was also under Treub's direction. In the interval of more than ten years that had elapsed since the first visit the number of plants had greatly increased and most of the island was covered with vegetation which began to show the characteristic formations which are now so conspicuous. The "*Pes-capræ*" formation, *i. e.*, the beach zone characterized by the predominance of *Ipomœa pes-capræ*, was well established, but the belt of strand forest now so marked upon the southern side of the island was entirely wanting in Krakatau, but the beginning of such a forest was found upon the neighboring Verlaten Island. Almost no trees were met with, and even shrubby plants were not numerous. The grassy "steppe" lying between the beach and the base of the cone was conspicuous and probably not very different from its present condition. The total number of vascular plants collected on this second ex-

pedition amounted to sixty-two, of which twelve were pteridophytes and fifty phanerogams. The ferns still predominated in number of individuals.

A third party visited the island in 1905, but the results of this expedition have not yet been published.

A very full account of the present flora is given by Ernst (pp. 37 to 48). In the three expeditions the results of which have been published a total of 137 species is recorded. While a very large majority of these are phanerogams, representatives of all the principal groups of plants have been collected. In the earlier expeditions the preponderance of ferns, as we have seen, was very noticeable, but at present this is not the case and they have largely given place to the more aggressive phanerogams. We collected only six species of ferns and one of Lycopodium, the wide spread *L. cernuum*, while on the first and second expeditions eleven species were noted, and although it is true that we failed to reach the center of the island, where in all probability other species would have been encountered, it may be noted that we collected seventy-three species of phanerogams against forty-eight species recorded at the time of the second expedition.

Of the lower plants only two species of mosses have been collected and a single species of antheroceros (this was found only on the second expedition). We found the two species of mosses growing fairly abundantly, but no liverworts. Whether the latter grow in the central part of the island remains to be seen, but it is highly probable that some of the very numerous species of Java and Sumatra will be found there. The scarcity of bryophytes is remarkable, as it is generally assumed that their spores are readily disseminated; and the contrast with the ferns which so quickly colonized the island is most striking. Three species of fleshy fungi have been collected and a considerable number of species of diatoms and blue-green algæ were among the earliest settlers of the island.

Professor Ernst made some interesting studies on the

bacteria, collecting from several places samples of soil which were placed in sterilized tubes. These were examined by Dr. E. De Kruyff, bacteriologist of the Agricultural Department at Buitenzorg, and the soil was found to contain the usual proportion of bacterial forms, both ordinary soil bacteria and putrefactive types. An interesting discovery was the presence of a new aerobic nitrogen-fixing bacterium, which was named *Bacterium krakataui*. *B. radicicola* is present in abundance in the root tubercles of the numerous leguminous plants which now abound on the island. It is evident that the different kinds of bacteria must have very early established a foothold upon the sterilized island surface and were no doubt among the factors which rendered the establishment of the higher types of vegetation possible.

A most interesting find was a single thrifty female specimen of *Cycas circinalis*. This tree had a trunk nearly two meters in height, and the size of the plant suggested that it was a survivor of the original flora; but Ernst states that this is impossible, as the portion of the island where it is growing belongs to the new shore formed since the eruption.

Agents in Distribution

Ernst has treated very fully the question of the agents by which most of the members of the new flora were introduced (pages 53 to 68). There seems no doubt that the earliest immigrants—bacteria, blue-green algæ, ferns and mosses, were wind borne, and the same is probably true of the first phanerogams found upon the island, composites and grasses, but other agents have been active in transporting seeds and fruits to the shore of the devastated island, and of these the ocean currents have probably been most important. There is no question that the fruits and seeds of the strand plants are probably all water borne, and Ernst called attention to the important part played by driftwood in introducing new plants whose seeds might have been lodged in the crevices in the

bark, or he even suggests the possibility of young plants being transported on uprooted trees. The shore of the island is covered with masses of logs and fragments of trees which might very well have brought with them not only vegetable immigrants, but animals as well. An interesting case was that of the two species of fleshy fungi, Polystictus, which were found growing upon logs lying on the shore, and whose mycelium almost certainly had been growing in the logs before they were drifted out to sea.

Birds have undoubtedly also played their part in the introduction of seeds, especially those of fleshy fruits such as the species of Vitis, common near the shore, and several species of figs found somewhat further inland.

The rapid development of the vegetation in the nine years between the visit to the island in 1897 and our visit in 1906, and especially the great increase in the forest vegetation, makes it evident that before very long the forest which originally covered the island will be again in possession. Already the belt of forest along the shore is working inland, and it is to be expected that the patches of forest in the ravines flanking the cone in the interior of the island are spreading shoreward, so that in the course of time the intermediate belt of grassy land will probably be completely obliterated and the forest will once more be in undisputed possession of the entire island.

A MALE CRAYFISH WITH SOME FEMALE ORGANS

PROFESSOR E. A. ANDREWS
THE JOHNS HOPKINS UNIVERSITY

THE crayfish to be described here was peculiar in being a male with some few of the external characters of a female. If by the term gynandromorph we understand an individual that shows both male and female organs in different parts of the body, though the normal individuals have but one set of sexual characters, we may call this crayfish a gynandromorph.

Compared with other known cases of mingled sex in the crayfishes this one is peculiar in being chiefly all male, while most of the other cases on record are predominantly female.

Before describing this crayfish it will be useful to recall that the sexual organs of crayfishes consist of the gonads, ovary and testis, their ducts, certain modified limbs to ensure the transfer of the sperm to the female from the male; and in the crayfishes of the genus Cambarus, a sperm receptacle upon the female in which to store up the sperm till the time the eggs are laid.

The ovary of the female is a median mass that becomes filled by the large eggs and from it an oviduct passes down on each side of the body to open out upon the base of the antepenultimate leg, right and left, as a rounded hole that is closed by an operculum, except at the time of egg laying.

The testis of the male is a similar but smaller body from which a convoluted duct leads down each side to open out on the base of the ultimate leg at the tip of a perceptible papilla which is turgid with the pressure of the blood.

The limbs of the female are reduced, or absent, upon the

first somite of the abdomen, while those on the second are like the following ones. But the limbs on the first somite of the abdomen of the male are quite remarkable conduits that conduct the sperm; and the limbs of the second somite are peculiarly adapted to fit against the first as a necessary part of this sperm-transferring apparatus. The limbs of the thorax may also be modified so that some of them bear hooks for holding the female.

In the case of Cambarus the female sperm-receptacle is a unique median pocket in the shell, which is of as much physiological necessity for the race as are the ovary, the testis and the male appendages that transfer the sperm.

The gynandromorphic crayfish to be described was a small sized and probably immature male of the species *Cambarus affinis*, taken in a lake at East Hampton, Conn., by Mr. Kenneth N. Atkins.[1]

The external appearance of this specimen was that of a male 55 mm. long with small chelæ only 30 mm. long, having the hand 15 mm. long and 5 mm. deep. The antennæ were 45 mm. long. The papillæ of the fifth or ultimate legs seemed normal. The second abdominal limbs were as usual in a male but the first were of the puerile or so-called second form of male limb very like that found in a young normal male five months old and 38 mm. long. The tips were blunt and there was a free joint above the basal joint. The attaching hooks of the third, or antepenultimate, legs were short and blunt, but normal for the young male. There were the usual long male hairs on the spine between the ultimate legs, and

[1] The finding of this species in this locality is of interest as bearing upon the geographical distribution of crayfishes. New England being singular in the fewness of its crayfishes, which are largely restricted to the drainage into the St. Lawrence, the question to be settled is whether the crayfishes are absent because they never got there or because some characteristics of climate, soil or biological environment are inimical to them. It seems that these crayfishes were first observed in this lake some nine years ago, being, it is thought, brought there by fishermen. Since these crayfish are fairly abundant there now this is evidence that crayfish can live in this region, and favorable to the idea that the relative absence of crayfishes throughout these states is due to their not having migrated in there.

no sign of any female organ, the sperm receptacle, anterior to it.

To these male external features there were added the two female openings on the antepenultimate legs. On the right the basal segment of the leg bore a well-formed normal female orifice, that is, a soft, round, depressable area, or operculum. This opened along the median edge as a curved mouth bounded by a narrow stiff rim of hard shell. On the left the opercular area was perhaps somewhat less perfect, its median side being more a straight line which opened as a mouth, and the curved bounds were more vague. The hard rim was thicker, apparently by the amount that the straight mouth should have been curved to make the normal contour.

On dissection the internal organs were found to be entirely those of a male, for the above female openings had no connection with the interior and there were no oviducts nor ovaries. On the right the operculum, when pushed in, showed a short conical pocket that received a needle point but appeared to end blindly as a mere thin chitinous continuation of the shell inwards. This pocket was flat. The mouth was a little more than 1 mm. long and the pocket slightly shorter than the mouth, on the right side. On the left the mouth slit led into a pocket of less extent.

The essential internal organs of this animal were the testis and the two efferent ducts. The testis was a median mass some 3 mm. long under the heart, with two anterior lobes about 2 mm. long rising upwards in front of the heart. Besides this well-developed part the testis was continued back over the intestine as a short minute membranous thread and forward between the stomach and the hepato-pancreas as a clear tubular membrane, or sterile part of the testis about 2 mm long, from the right and from the left lobe.

Where the right and left lobes joined the median lobe the different duct sprang out each side and, passing back alongside of the median lobe some 3 mm., went away at

right angles over the surface of the dorsal muscle-mass that comes into the thorax from the abdomen on the side of the thorax, without any coils or turns, some 4 mm. Each duct then descended in a slightly sinuous course to the projecting base to which the antepenultimate leg is attached, where it became thicker and, making a short semicircular curve, entered the basal joint of the leg and passed straight out to the tip of the papilla. The duct contained sperm.

Comparing these findings with the anatomy of normal young males and females of the same species, we see that in a male of 65 mm. killed in October the first pair of limbs on the abdomen have much more perfected tips and lack the joint near the base; while internally the sperm ducts that lie alongside of the median part of the testis are so coiled as to be there about 20 mm. long instead of 4 mm. The duct was also larger and contained more sperm. Allowing for the differences in size and in time of year, the two specimens are essentially alike and we may regard the abnormal one as perfect in all its male organs, though they had not reached their final form. Doubtless this male would have been able to transfer its sperm to a female in the proper season, that is, in the fall.

Serial sections of the testis show no indications of any hermaphrodite nature, no ovogenesis in any part. On the other hand, the different duct and the collecting tubules contain some nearly mature sperms. Some of the acini show spermatogonia with equatorial plates.

The two sham oviduct-openings of this specimen when compared with the real openings of a female of October, some 60 mm. long, show the closest agreement externally. But there is the fundamental difference internally that the normal mouth, instead of leading into a blind, minute pocket, continues directly as a wide and comparatively straight tube some 10 mm. upwards to the ovary.

In brief, then, this gynandromorph was a young male that would have functioned as such at the next breeding season, yet it presented two female characters, openings

as if to lead to ovaries, but with no internal connections and no discoverable use. These sham openings stand in the proper place for the oviduct openings of a female.

A review of the literature fails to show any abnormal crayfish with just these combinations of male and female characters; in fact, as before stated, most of the known cases are females with some male features. Recorded abnormalities of crayfishes include the cases of repetition of parts in one sex and the cases of mixtures of traits of two sexes. The former have been brought together by Bateson in "Materials for the Study of Variation," Macmillan, 1894, the latter by Hay in "Instances of Hermaphroditism in Crayfishes," Smithsonian Miscellaneous Collections, 1905.

In his monograph on the crayfishes of Pennsylvana Ortmann has recently described five additional cases in Cambarus, in which the external sex organs are more or less mixed and in part defective.

Bateson found that in 586 females of *Astacus fluviatilis* there were 23 abnormal cases. In these, besides the usual openings upon the bases of antepenultimate legs, there were one or two similar openings upon the penultimate, the ultimate or even upon all; making a maximum of three pairs of openings. Moreover, the oviducts generally branched so that more than one pair of oviduct openings might be functional, but in other cases the extra openings might end blindly and be of no use. Of 714 males only one was abnormal and that presented not a duplication, but a suppression of organs, having no trace of a generative opening upon the right side, while the sperm duct of that side hung blindly in the body cavity.

A real case of duplication of sexual characters in a male crayfish was recorded, in a rather inaccessible publication, the *Indiana University Bulletin*, by W. J. Moenkhaus, in 1903. He found in *Cambarus viridis* a male that had in addition to the usual first and second male limbs of the abdomen the third pair modified to exactly resemble the

second, in plan, and to differ from them but slightly in the detail with which this was carried out.

These cases of duplication of external organs must not be confounded with the gynandromorph here described since that has both male openings and female openings and not a mere duplication of the openings of one sex. There is so much difference between the male papillæ of the fifth legs and the operculate openings of the antepenultimate legs of the female that we must regard them as two morphologically and physiologically distinct organs and their occurrence upon the same animal is not the same thing as the duplication of one set upon one animal. This is true even if there were reason to suppose that both kinds of openings may have had some common origin in the past.

The cases of hermaphrodite crayfishes previously on record were considered by Hay along with most interesting new cases. It appears from his paper that there are in crayfishes no known cases of such complete, typical, gynandromorphs as that of the lobster described in 1703 as having both external and internal organs of the male on the left side of the body and of the female on the right. All crayfish gynandromorphs, but one, are really either males or else females as regards the gonads, and have added but some of the external organs of the opposite sex. One is a female with a little testis as well as external organs of the male.

The numerous cases of crayfishes from the southern hemisphere with the external openings of both males and females described by different authors are especially interesting as resembling the gynandromorph of this present paper, since it was found by Lönnberg,[2] that whenever the internal anatomy was made out, the animal had either a testis or an ovary, and if there was a testis the normal ducts led to the normal male openings, while the redundant female openings had no internal connections, though the testis did send out an extra duct towards the

[2] *Zool. Anz.*, 1898.

pseudo-female opening; while if there was an ovary the oviducts went to the normal openings and the extra male openings were of no use, though here again the ovary sent out a duct towards the useless male openings.

The extra openings, however, Lönnberg found to be shams, or closed openings, yet they look like the openings of the opposite sex.

This state of things, the perfect male or female with sham openings and pseudo-ducts of the opposite sex, seems to be the usual, if not the only, condition found in many species of the genus Parastacus, to judge from all the specimens that have been studied. The relationship between Parastacus and Cambarus is, however, believed to be so very remote that one can not suppose the present case of abnormality in a species of Cambarus has any genetic connection with what seems to be the rule in many, but not all, species of Parastacus.

The other recorded gynandromorphs are one specimen of Astacus and fourteen of Cambarus, and all except one are females that have some male characters added. The superfluous male characters are sometimes but the modification of the first abdominal limbs to resemble those of the female, in others both these and the following limbs are just like the male limbs. In one the male attachment hooks, and the male openings and even the hirsute spine posterior to the somite of the sperm receptacle, that is, all the external characters of the male, are present along with normal ovary and oviduct.

This last was the most hermaphroditic of all known crayfishes. It was the female *Cambarus affinis*, 106 mm. long, described by Hay. This seemed externally a male and attempted conjugation with a female, having a good set of male external organs. But internally it had a large ovary with nearly mature eggs and two perfect oviducts. The specimen was thus deficient in lacking the sperm receptacle that a female of this kind of crayfish should have in order to get the eggs fertilized. In addition to the ovary there was a small testis, on the right,

with a duct leading to a single male opening on the ultimate leg. Though no sperm was present it seemed as if sperm might have been made. It appears that this individual could have been of little or no use to the race.

With this exception all sexually abnormal crayfishes, as far as known, are either males or females with either some duplication of organs that belong to that one sex or else the addition of external organs of the opposite sex. But in Parastacus there is also some duplication of internal ducts, which needs additional investigation to show how far it is duplication and how far it may be the addition of ducts of the other sex. As far as Lönnberg's observations go the extra ducts were like the normal of that sex and not like those of the other sex.

The fact that the male may have merely the external openings of the female sex without any internal female organs shows that the gonad is not necessary as a stimulus for the making of the external organ, that the external organ is not correlated with the gonad by any internal secretion or other means, necessarily. At the same time Parastacus shows that when there are extra openings, or rather sham openings, the gonad sends extra ducts towards those openings so that there seems a correlation between the gonad and the external organ that belongs to the opposite sex. However, Lönnberg found in some of the testes of Parastacus objects that he thought might be eggs; so that the purity of the gonads is somewhat doubtful.

There is a possibility that these males may have had enough development of a hermaphrodite gonad to supply a stimulus to the surface that would make the external female organs begin to develop in the right place for a female having ovaries, though the gonad was essentially male.

The gonads of crayfishes are late in becoming visible in the ontogeny of the individual and the external organs do not show till the eggs have hatched and passed into the third larval stage, after two moults. Whether these

external organs would develop at all without the internal gonad can only be determined by future experiment, but the abnormal cases above cited show that the external organ may be formed without the gonad of that sex to which the external organ ought to belong and make it probable that the external organs and the gonads are so independent that we need not suppose one leads to the formation of the other.

The sex of the crayfish is not merely the possession of egg or sperm, but of something made evident in a variety of places over the body, as sex organs that are accompanied by the necessary reflexes and instincts to use them.

That the sex is rather intimately dependent upon function seems to be indicated by the occurrence of the two forms of male, known as the first and second, which alternate in such a way that at the breeding season the external organs of the male are perfect, while at another time of year the same male has relapsed into a juvenile state in which the sperm transfer organs are as they were in youth and probably of little or no functional value. These morphological changes are made possible by the shedding of the shell and the growth of what is practically a new organ.

We have then some reason for supposing that back of the visible sex organs there is some state or condition of the organism that can at least modify the structure of the sex organs.

Nothing is known as to the origin of these gynandromorph crayfishes. But regarding the eggs as at first able to make either male or female, or make more than one individual under certain circumstances, the gynandromorph may be looked at as a partial realization of the entire set of possible organs. The causes may lie in physiological states present at various stages of ontogeny. Where a whole species is gynandromorphic the egg may be predestined in the ovary to produce a mixture of organs. When only an occasional individual has

a few external organs added to the normal set the causes may lie in conditions not found till late, after fertilization.

Just as the determination of sex may be due to different conditions in various animals and plants, so the repression or the expression of one or another sex organ may be due to diverse causes acting at various periods of ontogeny, and not to any single factor. Moreover, we do not know how far the gynandromorph may be the result of aberrations independent of the causes of determination of the gonads.

However amongst the insects, where gynandromorphs are well known, there are reasons for restricting our surmises as to the time of origin of the mixed expression of sex organs. Here the mixing seems to be associated with the period of fertilization. In the honey bee the sex is determined, apparently, in fertilization and the phenomenal cases of gynandromorphs, such as those studied by V. Siebold in 1863, in the Eugster hive, have often been explained as due to abnormal fertilizations. This interpretation has been most acutely elaborated by T. H. Morgan on the basis of the facts of experiments upon echinoderms and the results of Toyama upon hybrid moths. He is finally led to the view[3] that the egg nucleus by itself would produce male, the sperm nucleus by itself also male, but the two combined produce female. The gynandromorph would be the result of polyspermy. It would be a sort of combination of individuals, the one female, arising from the part of the egg containing the fused egg and sperm nucleus; the other, male, arising from the part of the egg in which extra sperms developed without contact with the egg nucleus. The female parts of the gynandromorph would have two parents and should be mixed in a hybrid, the male parts would have but one parent and should be pure in a hybrid.

The hypothesis of polyspermic origin of gynandromorphs might be applied to the crayfish with the common assumption of two sorts of sperm, male producing and

[3] This journal, November, 1907.

female producing.[4] We assume that every egg is fertilized and will be male or female according to the sperm that unites with its nucleus. But a gynandromorph might arise by adding to the male or the female some organs of the opposite sex due to the independent development of the opposite kind of sperm in parts of the egg. All sorts of gynandromorphs might be imagined upon this basis. Moreover, we might assume the abnormal cases of duplication of sex organs in one individual, such as studied by Bateson, to be due to the independent development of sperms that happened to be of the same kind as the one that fused with the egg nucleus. In theory we might even refer the doubleness of organs not concerned with sex to some sort of super-fertilization.

Whether such hypotheses have any value may be determined by future experiments in the cross breeding of crayfish. Such experiments may enable us to decide whether gynandromorphs arise before, during or after fertilization and may throw light upon their causation. The crayfishes in this part of the world, are especially well adapted to these experiments, for if crosses can be obtained at all, we may expect to distinguish between pure and mixed sex organs, since both the male and the female have external organs that are at the same time essential sex organs and characteristic specific characters.

Meanwhile the totality of facts known seems to mean that the gynandromorph crayfishes are caused by unknown disturbances, which may happen at various periods of ontogeny, though probably more often in the ovarian egg; that these disturbances may have no connection with the gonads; and that if in some cases the disturbances are possibly associated with polyspermy, in general they seem more fundamental and deep seated amidst the causes of symmetrical form within the egg.

BALTIMORE,
January 11, 1909.

[4] In some crayfish there are visibly different forms, some are wound clockwise and some counter clock, some have more and others less rays.

PRESENT PROBLEMS IN PLANT ECOLOGY[1]

IV. Problems of Local Distribution in Arid Regions

PROFESSOR VOLNEY M. SPALDING

Desert Botanical Laboratory

The physical conditions prevailing in arid regions are such as render it unsafe to admit without further investigation generalizations regarding their plant life which have been drawn from studies conducted elsewhere. This is sufficient justification of an attempt to analyze certain problems which confront the student of desert ecology in his efforts to apply knowledge or principles drawn from previous experience. These problems have the advantage of a certain clearness of definition, which corresponds in a way with the sharp features of the desert and its characteristic vegetation. Their solution may involve great difficulties, and some of them, with our present methods, may be incapable of solution, but they are, at all events, capable of clear statement.

In the attempt to present such a statement, which may or may not prove successful, I shall for the present limit the discussion to the desert country of the southwestern United States, for the sufficient reason that my own studies have been conducted in that region; and I shall omit all consideration of the higher elevations of the mountains, which, though in the desert, are not of it; so that whatever is said at this time will be understood to apply to the floor of the desert, that is the great plateaus and valleys which from Texas to California lie between the mountain peaks and ranges, together with the long slopes and low hills which border them on every hand and form the natural approach to the mountains.

[1] A series of papers presented before the Botanical Society of America, at the Baltimore meeting, by invitation of the council.

Proceeding in a manner that will be indirectly a record of personal experience, one of the first questions presented to a student of desert botany is this: What are the conditions that determine the successful occupation of a desert habitat by certain plants, but prevent its occupation by others?

It will be necessary at the outset to understand what is meant by a desert habitat, since on this point the popular conception—and possibly that of some botanists—is not clear. There is as much difference between habitats in the desert as in any other region, possibly more, and their definiteness of location and relative sharpness of demarcation form one of the most striking and characteristic features of arid regions. The rivers of the valley trough, such as the Santa Cruz, the Gila and Salt Rivers in Arizona, though inconstant, are none the less the main drainage channels between the adjacent water sheds. Along their banks water-loving willows, cottonwoods and arrow-weed find a congenial home. The adjacent flood plain, with its water table within reach of their roots, is the natural habitat of the mesquite and some other semi-mesophytic species. Within its limits the areas known as salt spots are inhabited by various halophytes, especially by species of *Atriplex* and *Suaeda*. Just beyond the flood plain is the long slope, a most characteristic feature of desert topography, which rises slowly to the foot of the mountains, often miles away, its soil and drainage conditions presenting a sharp contrast to those of the flood plain, and its vegetation being correspondingly different. The low outlying hills, in their turn, present quite as marked peculiarities of soil, and furthermore introduce differences of aspect which are correlated with marked differences of vegetation. In short, the habitats of such a desert region as that of southern Arizona, as far as edaphic relations are concerned, present conditions which vary all the way from distinctly hydrophytic to extreme xerophytic, and all these may be in close proximity.

For all these habitats the fact is to be emphasized that the general climatic conditions are the same, and it is important to note that not a few of the plants which grow where a sufficient or even abundant water supply is assured are nevertheless marked, as a rule, as plants of an arid region by their coriaceous, hairy or otherwise xerophilous leaf structure. The point to be specially noted here is that while plants of the arid, or semi-arid southwest grow in a great variety of habitats, some of which are by no means dry, all are subject to the severe conditions of a desert climate, especially intense insolation, low percentage of atmospheric moisture, and drying winds. The problem, therefore, of the occupation of any one of these habitats is successfully met only by those plants that are already adapted, or are capable of individual adjustment to the dry air and hot sun in which they must live; all others inevitably fail.

This will be made clear by reference to the introduction, or attempted introduction, of various cultivated plants, a subject which presents a most instructive history. The yards of Arizona cities constitute an experiment station in which year by year, at private instead of public expense, the availability of one species after another for desert planting is being determined. From the great number of plants successfully cultivated there seems, at first sight, to be sufficient justification for the reiterated assertion that anything will grow here if you only give it water enough, but closer attention to the actual facts of the case makes it evident that this statement is true only in part, and that there are many plants that will grow only indifferently or not at all under the atmospheric conditions which prevail here, especially in the summer time. To give a few examples, geraniums, the universal easily raised plants of moister regions, are very uncertain, some varieties accommodating themselves fairly well to the desert air, while others fail altogether. Cannas and gladioli, which grow side by side in the east, part company here, the former making a good growth in

Arizona gardens, the latter failing altogether. Those who have handled roses for a period of years have learned what varieties may be expected to do well in the dry air of the desert, and what ones may be counted out, and so on through a long list of plants which, by knowledge gained in the costly school of experience, are coming to be depended on, or are being rejected one after another, as they are found to be unsuited to the environment into which they have been brought. Thus, in a purely empirical way, it has been found that many plants successfully cultivated in regions of greater atmospheric humidity make an entirely normal growth in the desert, if their roots are well supplied with water, but that others, however well cared for in this respect, either fail completely, or come short of making a healthy growth, and that this is especially true in the summer months when desert conditions are most pronounced.

With the accumulation of such facts the more evident does it become that a very complicated problem is here presented. Why is it that one plant, properly watered, does well in the desert, while another, though treated in the same way, makes a poor growth or fails altogether? At first thought it would seem as though there must be a difference in the capacity of the root systems of the two plants for absorption, and that this may be a sufficient explanation of their different behavior; but it is evident on consideration, that with precisely the same capacity for root absorption, a plant in which transpiration is successfully regulated may thrive in an atmosphere in which one subject to excessive transpiration will perish. The most elaborate experiments and the most exact determinations of rate of absorption—assuming that such determinations are possible—would be very likely to throw no light on the problem. Comparisons of the transpiration rate of the plants in question appear more promising, but the same difficulty arises in an attempt to pursue the investigation along this line, for there is no reason to suppose that two plants of widely different rates of trans-

piration can not successfully occupy the same habitat if their capacity for root absorption differs in the same ratio. But supposing that with infinite patience and with a reasonable approach to accuracy both sets of physiological data have been determined, we are still, quite possibly, entirely in the dark as to the real cause of the different behavior of the plants under investigation. It may be in their case that the whole matter of absorption, conduction, and transpiration is beside the mark, and that certain plants can not succeed in the desert because the intense insolation exerts directly a prejudicial influence to which they have not become inured. The intricate nature of the subject is apparent, and it is also evident that there is little encouragement for any one to take it up who has not had extended training and thorough equipment for physiological research. Yet with all its difficulties the problem is an attractive one, and the abundance of material to be had in any desert city, together with the great mass of data that has accumulated in the hands of horticulturists and at the experiment stations, offers the best of opportunities for extended and fruitful work.

If, as we have seen, the different deportment in the desert of plants growing, or having the opportunity to grow, side by side in well watered ground, is an exceedingly complicated matter, by how much are the difficulties increased when we pass from a habitat of uniform and highly favorable conditions, to the various and often extremely trying conditions which prevail in different neighboring habitats, such as the dry slopes underlaid by caliche, the salt spots and others. If the case of a plant growing in well watered soil may become desperate because of the scorching winds or the intense insolation to which its top is exposed, what hope is there for one that assays to grow where both dry air and dry soil present the supreme test of endurance? As a matter of fact only relatively few species meet the test successfully, yet there are some that do, and they present some of the

most instructive data yet derived from the study of desert plants.

But little reflection is needed to arrive at the conclusion that the classical question regarding the relative importance of physical constitution and chemical composition of the substratum to plant growth—though like the poor it promises to be always with us—does not, and can not reach the heart of the problem. For every plant which successfully holds its place in a true desert habitat there is a delicate balancing of the regulation of transpiration, the power of absorption, the capacity of the conducting system, the presence or absence of storage tissues, and, we may well believe, the possession of protoplasmic properties which contribute to its powers of endurance. This being the case, it would seem that in future, investigations of the habitat relations, of desert species especially, must be directed mainly to the plant itself. The advantage of a thorough knowledge of soils is too obvious to call for comment, but it must be remembered that we are as yet only at the threshold of a greater and more promising work, namely, the investigation of the physiological requirements and capabilities of plants that can grow in a true desert habitat as compared with those that can not. In such comparative study lies, as it seems, the hope of real progress. It is impracticable for any investigator, at the present time, to mark out a straight path for others to pursue, and it would very properly be regarded as an impertinence were he to attempt this; yet there are certain obvious suggestions that may be offered.

In the first place, important results have already followed the simplest experiments and observations when these have been conducted with exactness and with a definite end in view. To refer to a specific case,—Professor Thornber, of the University of Arizona, undertook a few years ago to compare the habits of certain desert plants as regards germination. It was found that while the seeds of some species germinated at a given

temperature, others could not be made to do so until they had been subjected to temperatures approaching the freezing point. These latter were seeds of winter annuals, and by this method a fundamental physiological difference between them and the summer annuals was established. Doubtless an indefinite amount of instructive and necessary work remains to be done in this direction, but the key to the situation was found in carrying out the simple experiments described. Again, partly as a relief from severer work, Dr. Cannon undertook, in the midst of his investigations at the Desert Laboratory, to map the distribution in the soil of the roots of some of the plants growing in the vicinity. Hardly was the work well in hand, and the root topography of less than half a dozen species mapped, when it was found that the clue to certain facts of distribution, blindly observed up to that time, had been discovered. I have spoken of this in more detail in another connection.

Obviously it is indispensable that determination of physiological data and of those belonging to the physical environment should proceed step by step together; and nowhere is this more strikingly true than in the investigation of soil relations. To refer to one more case of recent experience,—within the past year Dr. Livingston has determined the percentage of soil moisture present in soils obtained from each of the topographic areas of the Desert Laboratory domain and the adjacent flood plain of the Santa Cruz River. His studies were conducted independently, though naturally not in ignorance of ecological studies which were being carried out at the same time on the same ground. It now appears that a well-nigh perfect correspondence exists between the two sets of facts obtained by independent workers, so perfect, in truth, that a causal relation offers the only satisfactory explanation. The accumulation of physical data, however, has proceeded so far and so satisfactorily that the successful conduct of this line of investigation may be regarded as assured, but for the plant the relations

are more complicated, and their investigation correspondingly more difficult. It seems likely that in the study of ecological relations from the side of the plant we shall employ more and more the methods and conceptions of physics and mathematics, but the fact is too patent to call for argument that neither now nor hereafter can these methods and conceptions be employed exclusively. In fact there has never been greater need than at the present time for exact observation coupled with correct judgment, and these can never be replaced or superseded so long as this department of botanical investigation continues to be cultivated. This will receive additional emphasis in the following division of the present paper.

The relations of desert plants to each other present a chapter, the importance of which has been unduly minimized until the general impression, even among botanists, seems to be that desert plants are to be studied only in relation to their physical environment; they are thought to grow so far apart, in "open" associations, that they are quite uninfluenced by each other's presence. Like other erroneous or incomplete conceptions, this may be true in part, especially where the most extreme desert conditions prevail, as for example in parts of the Colorado or Mojave Deserts, but in the great semiarid region of the southwest, taken as a whole, it is most misleading. The Desert Laboratory of the Carnegie Institution was located where it stands on account of the great natural advantages which the region and locality offer for the study of desert plants in place. yet I venture the assertion that over at least nine tenths of the area of the laboratory domain the establishment of a plant in the place which it occupies is conditioned quite as certainly by the influence of other plants as by that of the physical environment. It hardly needs more than simple observation to convince one that severe competition is the rule, though naturally its severity is heightened and the result hastened by the prevailing adverse physical conditions.

Beginning with some of the most obvious cases, the winter annuals of southern Arizona present an instance of as unmistakable competition of individuals with individuals and species with species as can be found in the eastern forest region of the United States. As the warmth of spring follows the winter rains the ground is thickly carpeted with *Amsinckia*, *Pectocarya*, *Bowlesia*, and various other herbaceous plants, which stand thick together and present to the eye the familiar crowding which is seen in a field of grain too thickly sown. Certain individuals dwindle and finally die, robbed of water, food and light by their stronger competitors. It might be interesting to repeat the experiment in the laboratory and to tabulate the results statistically, but it could hardly add to the conclusiveness of the demonstration. The same is true of the manifest competition of species with species, as seen for example in the occupation of relatively extended areas by some of the perennial grasses which, but for their presence, would certainly be covered, as the adjacent areas are, by a thick growth of other plants. Here the actual advance of the grasses from year to year may be observed, and such observations for the sake of more definite statement are now in progress on the Desert Laboratory domain. Convincing evidence of competition is thrust upon one's attention in passing from the desert to areas beyond its borders, and if the transition is abrupt, as for example on the western edge of the Salton Basin, where the desert abuts almost upon a mountain wall, the case is all the more striking. In this instance a straight course of less than five miles brings one from the actual desert, with its characteristic sparse growth of salt bushes, creosote bush, galleta grass, and the like, to the chaparral of the mountainside. Along the way the desert species fall out one by one, and are replaced by elements of the chaparral. As far as can be judged by their habits elsewhere and from their known range in altitude, there is absolutely no reason for this, except their inability to compete with plants of the cha-

parral, which, however incapable of normal development in the desert, hold their own ground, where the conditions are less strenuous, so tenaciously and completely that the desert species make no headway against them.

This, of course, is an interpretation merely, but with such an accumulation of evidence we are now in a position to proceed with the problem along definite lines with the expectation of definite results. Sowing together seeds of desert and other plants, the transference of individuals to denuded areas beyond their natural limits, and multiplied comparative observations of the deportment of different species on the "edge of the desert" are simple and obvious methods of procedure at the outset. Some of this work has already been done, enough to convince those engaged in it that in general the problem of the successful occupation of a desert habitat involves the recognition of actual competition on the part of its would-be occupants, a competition severe enough in some quarters to set up a barrier beyond which, in the midst of otherwise entirely favorable environmental conditions, they can not pass.

In their relations to each other, desert plants frequently exhibit not merely competition but accommodation. This has been clearly shown by recent studies of the root systems of certain cacti and other plants by Dr. W. A. Cannon. To take a striking example—superficial observation of the association of the sahuaro (*Cereus giganteus*) with one of the palo verdes (*Parkinsonia microphylla*) and some other shrubby perennials gives no satisfactory clue to the reason of this relation, and the common explanation that they are plants of similar biological requirements, and therefore grow together, is altogether inadequate and in part misleading. The careful study, however, that has been given to the root systems of these plants brings out the important fact that they grow close together by virtue of simple accommodation, which enables them to utilize to the utmost the scanty rainfall. The roots of the sahuaro are spread

just beneath the surface of the ground, where they take up and promptly pass on to the storage cells of the trunk the water brought to them by every light rain. The roots of the palo verde, on the other hand, extend much more deeply into the ground, and are in a position to utilize the water which soaks down to lower levels after heavier rains. Thus the sahuaro profits by all rains, light and heavy alike, while its constant companion, the palo verde, is free from all competition on its part for the water which penetrates to lower levels. Much the same thing is seen on the flood plain of the Santa Cruz and other rivers, where the mesquite, with its deep roots reaching to the water table, is associated with *Bigelowia* and other plants, the roots of which extend to relatively shallow depths. In short, it appears that just as in a tropical forest the vegetation occupies successive "stories," so here the root systems of various plants habitually reach to different depths, and thus enable at least some species that would otherwise compete with each other to live in close and advantageous association.

From what has been said, it is evident that in the successful occupation of a desert habitat the mutual relations of the associated species play a highly important part. It is not quite easy at this stage of progress to point out the exact steps by which these complicated relations are to be determined and estimated; meantime the homely and effectual method of patiently gathering the data that are obtainable by careful observation is open, and as far as it has been pursued has yielded valuable results.

The broad general problem of the local distribution of desert plants is necessarily approached along the several lines that have been indicated. As we have seen, atmospheric conditions, whether of intense insolation or extreme dryness, that obtain in arid regions are limiting factors which many plants successfully meet, but to which many others succumb. There has been great need of more practical methods of determining and estimating

the influence of atmospheric factors, and it is a matter of congratulation that the methods devised by one of the participants in this discussion, already widely in use in different parts of the United States, promise to meet this need to a degree that could not be hoped for at an earlier period. But it is never to be forgotten that under the same atmospheric conditions, and with equal chances in other respects, the deportment of two plants side by side, their capacity for adjustment let us say, is so different that the essential problem lies first of all in the physiological capabilities of the plant itself.

More strikingly true, if possible, is this seen to be the case when the relation of desert plants to the soil is considered. It is well that so much soil work has been done, that we have soil maps, that determinations of water capacity and other physical as well as chemical characteristics have been ascertained in so many habitats, and that we have a growing literature embodying observations of the relations of plants to underlying rocks, in short that the substratum has been the object of so long and so thorough study; there is no danger that we shall have too much of this, but there may be danger that we may sometimes forget to place the emphasis where it belongs, namely, on the fact that every species and every variety of plant is a law to itself in its relations to rock or soil. It is true enough that the different percentages of alkali salts at different distances from the center of a salt spot stand apparently in causal relation to the growth of different plants in corresponding concentric zones, but it is equally true that this zonal arrangement is also the visible expression of the capacity of these different plants to cope with the conditions there existing, and of this capacity, if it is to be expressed, as some day it must, in physical measurements, how inadequate is our knowledge. How greatly we need to really know the physiological constants, not of one but of many desert plants.

It is in the same line of thought, and with the same purpose, that I have referred to the inadequate concep-

tion according to which the relations of desert plants to each other have been so persistently overlooked or at least underestimated. It may now be set down as an established fact that over a large part of the arid or semi-arid territory of the southwest, competition on the one hand and accommodation on the other have much to do with the association of plant species and the density of the plant cover. Far more, it would seem, than has usually been thought, the character of various associations in this region is determined not simply by the physical but also by the living environment. More than ever too, it is plain that the path of progress lies in the direction of applying to the plant itself, in its natural surroundings, the experimental methods of the physical laboratory. Notable and fruitful beginnings have been made in this direction, but one who has attempted quantitative work with the sahuaro or ocotillo in the open need not be told that it involves difficulties not presented by seedlings of *Vicia faba* grown in pots, and that progress will necessarily be slow.

Thus far adjustment and adaptation have not directly entered into the discussion, although a moment's thought shows that all the paths along which we have come converge right here. If one variety of geranium flourishes in the desert air, while another by its side dwindles and dies, we can only say at present that the latter is not "adapted," or is apparently incapable of "adjustment" to the atmospheric conditions in which it has been placed. We find that plants growing in the wash near the Desert Laboratory do not, as a rule, succeed in gaining a foothold on the long slope leading to the hill near by; they are not adapted to the soil conditions there existing; but the creosote bush, which makes its home on these slopes, grows—thanks to its capacity of adjustment—even more luxuriantly in the wash than on its own domain. Similarly, certain plants of the salt spots grow better beyond than within their limits; they have become adapted to large percentages of alkali salts, but their capacity of

adjustment is such that they grow just as well or better along an irrigating ditch carrying fresh water. Various other plants in the immediate neighborhood have not become adapted to the conditions prevailing in the salt spots, nor do they appear capable of adjustment to them, and accordingly are not found growing in such places.

We need not multiply citations of these familiar cases. Adaptation and adjustment have long been words to conjure with, out of the desert as well as in it, but we have made so little real scientific progress in the definition and determination of the things for which they stand, that some of our foremost students of ecology seem ready to abandon the effort, while others apologize when they use the terms, as if they were myths and had better be left alone. But nothing is gained, and much may be lost, by this method of procedure. We are face to face with a great body of phenomena of the most striking character, in connection with which these words are fittingly employed. We can not ignore the existence of the facts, and as scientific men we can not let them alone, while they insistently rise at every turn in our pathway and demand investigation. True it is that they bring in their train whatever is fundamental in biological inquiry —heredity, the direct influence of the environment, and differences in the properties of protoplasm in different plants. It is not customary, however, in laboratories worthy of the name, to shun investigations that approach to the deep mysteries of life. There is every reason why students of ecological problems should seek, not shun, this difficult but hopeful line of study. I say hopeful advisedly, for within the past three years there have come under my observation various definite cases of adjustment in plants, some of which have been accurately measured, correlated with external factors, and expressed by curves. Though essentially more difficult, there is no reason, as far as now appears, why the different degrees of adaptation of two species or varieties to a given external factor may not be similarly determined and

graphically represented, as the expression of a definite difference of physiological activity, as shaped by heredity, in relation to that particular factor. Very little, as far as I am aware, has yet been accomplished in this direction, but it is a way that is wide open, and one that should attract those real investigators who, knowing difficulties, do not shrink from them.

We have considered in a way far from exhaustive some of the problems which specially interest the student of desert ecology, but which in their broader relations are not confined within geographical limits. In the efforts now being directed towards their solution the trend, as it appears to the writer, is not so much away from any previous form of thought or method as towards the wise and persistent use of every means that promises results. Progress is certainly being made in the direction of greater exactness; we are learning something of the possibilities of well-directed cooperation; and in these and other ways in which "science returns to the obvious"—to use the apt words of Francis Darwin—is an encouraging promise for the future.

PRESENT PROBLEMS IN PLANT ECOLOGY

V. The Relation of the Climatic Factors to Vegetation

PROFESSOR EDGAR N. TRANSEAU
Eastern Illinois State Normal School

1. *The Recent Advance in Point of View.*—Perhaps the most interesting and important advance that has been made during the last decade in the study of the relation of plants to environment is in regard to the point of view. It is difficult to say just when the movement began, but it is assuredly true that it has only recently gained recognition. To a certain extent the movement has involved the substitution of the ecological for the floristic method in geographic problems involving climate. It has resulted in a general dissatisfaction with the older descriptive methods and has tended toward a better appreciation of the value of exactness both in the delineation of vegetation and the quantitative analysis of environmental complexes. The movement has further brought to our attention the necessity for investigating vegetation processes by experimental methods comparable to those by which plant processes have long been studied. As I see it, however, these are secondary phenomena attending the substitution of dynamic and genetic views of vegetation for the century-old static conception of plant distribution.

Fourteen years ago it was possible for one of the most prominent students of the North American biota to say:[1]

It appears, therefore, that in its broader aspects the study of the geographic distribution of life in North America is completed. The primary regions and their principal sub-divisions have been mapped, the problems involved in the control of distribution have been solved, and the laws themselves have been formulated.

[1] Yearbook, U. S. Dept. Agric., 1894, p. 214.

Such a claim could have been made only for a static system, since a genetic conception of the problem necessarily involves the indefinite postponement of the approach toward a final solution.

The appearance of the classics of Warming and Schimper served to impress all with the inherent complexity of the problem. We are no longer deeply concerned with the discussion as to whether temperature or moisture is the more important geographic factor. Neither do we hope to erect a stable system of geographic divisions upon either of these bases. When we recall that for North America alone not less than sixty different proposals of geographic zones and regions have been published during the last century, the futility of the point of view which disregards all but one or two climatic factors and emphasizes boundary lines, must be apparent. But we shall be still more impressed with the inadequacy of these proposals if we attempt to relate the actual distribution of plants or plant formations to these "regions."

Recently there has been a rapid increase of local ecological studies in which the successional processes of vegetation have been emphasized. These studies have apprehended to a greater or less extent the dynamics of the habitat and the plant formation. The separation of the local vegetation into stages has assumed the dominance in each, of a distinct complex of environmental factors. The occurrence of distinct boundaries has neither been assumed nor insisted upon.

Local studies, however, can not lead to general conceptions of vegetation unless compared and united into larger units. This brings us to the fact that the larger units generally recognized are transcontinental zones and regions. But zones and regions are static entities. They are developed upon assumptions wholly different from those upon which the local studies have been founded. Usually in zonal classification temperature is recognized as all-important and rainfall an unfortunate disturber of symmetry. Not a few are based upon phenological as-

sumptions long since proved untenable or still awaiting experimental evidence. In other words, the succession of local plant formations which has consciously depended upon changes in the concomitant action of many soil, climatic and historical factors, is made to fit into a larger unit whose fundamental basis is a single or at most two climatic factors. It is to be noted further that the problem most debated in connection with zonal arrangements is the boundary; that the term "zone" implies uniformity of structure and homogeneity of composition. But the most striking fact about the geographic distribution of individual species is their dominance in some region and their decline in importance and frequency as we depart thence in any direction. Plant formations in their distribution show the same phenomenon. Further, it appears that the optimum areas of scores and hundreds of species nearly coincide. In brief, actual plant distribution, through its lack of uniformity and homogeneity, its tendency to concentric dispersal, and the coincidence of the optimum areas of many species, seems to demand larger units in harmony with the processes, structure, composition and origin of their components. Whether we choose to call them "centers of dispersal" is of small moment, as compared with the recognition of the fact that zones and their sub-divisions are not natural organizations of plants or plant formations. Of course, this criticism does not refer to the use of the very convenient expressions of certain spatial and temperature concepts, viz., torrid, temperate and polar zones.

The unsatisfactory character of zones as a basis for classification is felt also by students of climatology. Especially is this true of the classification of the climatic types prevailing on continents. The schemes of Hult (1892–3), Koppen (1900), Supan (1903) and Herbertson (1905) are especially interesting in this connection.[2] Further, the provinces pointed out by Supan for North

[2] Ward, R. DeC. "Classification of Climates," *Bull. Amer. Geog. Soc.*, 38: 401–412, 465–477, 1906.

America show a remarkable coincidence with the natural vegetation centers. If future work both on climate and plant distribution should bring these fundamentally different view-points into essential agreement we should have the possibility of a completely dynamic and genetic system of vegetation and climatic units.

2. *Sources of Error in Applying Climatic Data.*—One of the sources of confusion in the use of the climatological data supplied by the Weather Bureau, in connection with vegetation studies, lies in the placement of the instrument shelter. The data derived recently by means of recording instruments placed in various topographic situations, show such great comparative variations, that the applicability of meteorological records made under the conditions represented by some of the weather stations may be called into question. Fortunately descriptions of the climatological stations of the United States are now available[3] and selection of stations which truly represent the conditions of at least one local habitat may be made.

A second source of error in the comparison with vegetation of climatic data as represented on charts is the fact that the means do not always represent actual local conditions, but may have been corrected for altitude above sea level. Such corrections, however, have not been made, except in the case of the barometric pressure maps, in the recent climatological bulletin of the Weather Bureau.

3. *Recording Instruments for the Measurement of the Climatic Factors.*—The increasing number of those who are attempting to secure by means of recording instruments, habitat data regarding temperature, relative humidity, etc., is the most hopeful sign of progress in the solution of the climatic problems of plant distribution. We now have fairly satisfactory recording instruments for temperature, humidity, rainfall and sunshine. The porous cup atmometer recently added to this list places

[3] Henry, A. J. "Climatology of the United States," Bull. Q, U. S. Dept. Agric., Weather Bureau, 1906.

at our disposal a recording instrument whose importance can not be overestimated. Because of its directly applicable data, its slight cost and ease of manipulation, it may well take precedence in comparative habitat investigations.

The greatest desideratum in the way of habitat study now seems to be an instrument for the measurement of light values. It seems probable that the effects of the varying light intensities and qualities in the habitat are generally underestimated at the present time. The comparative studies already made with actinometers and photometers are suggestive, but the value of the data as indicative of relative light conditions from the standpoint of vegetation is open to serious question. Thus far photographic papers have been most generally used. Aside from the high percentage of error attending the matching with standards of the colors developed, these papers are almost wholly affected by the most refrangible rays of the visible spectrum. Plant functions in general find their optima among the least refrangible rays. Owing to selective absorption, a decrease in the intensities of one portion of the spectrum does not necessarily imply a similar decrease throughout. The objection urged against photographic paper also holds for the use of other substances which develop precipitates or gas pressure under the influence of light. Unless papers can be devised which have an increased range of sensitiveness and which can be used in connection with color screens, the continuance of actinometric measurements in habitats seems almost a gratuitous pursuit.

Naturally the spectro-photometer has been suggested for overcoming this difficulty. By means of photographic methods, in which a diffraction grating is used for the dispersion-piece and photographic plates of known sensitivity to the various light rays, more accurate results might be obtained. The difficulties of manipulation, how-

ever, seem to preclude the use of this method at the present time.[4]

The method suggested by Zederbaur of using a spectrophotometer in connection with colored prisms and a standard lamp has been hailed by some as a solution of this problem.[5] It also involves several important sources of error, but these may not prove to be insuperable. This method has the great advantage over the actinometer in that it takes into account light quality. With certain modifications, some of which are suggested by Zederbaur, this instrument may prove to be a step toward a better means of light measurement.

4. *Some Climatic Problems of Vegetation.*—But even if the time is approaching when it may be possible to obtain both qualitative and quantitative estimates of the climatic factors related to vegetation processes, we should regard this merely as a preliminary to more important investigations.

We have as yet almost no observational or experimental data from a modern point of view, on geographic variation as related to climate. The reports concerning the results of the cultivation of certain varieties of agricultural and horticultural plants suggest a large field for the application of experimental methods.

A fundamental consideration in experimentation along this line is the use of pedigreed plants. It seems possible that many of the discordant results obtained by physiologists may be traced to physiological races within the species. The use of seeds from the same plant, branch, or fruit is not sufficient caution unless the pollination has been guarded. Where the growth of such large numbers of plants as would be essential to an experiment in geographic variation is necessary, the results could have little value unless the plants used had been analyzed by

[4] Wallace, R. J. "Studies in Sensitometry," *Astrophysical Journal*, 25: 116, 1907.

[5] Zederbaur, C. "The Light Requirements of Forest Trees and the Methods of Measuring Light." English translation. *Forestry Quarterly*, 6: 254, 1908.

scientific plant-breeding methods and been shown to consist of an elementary species or variety. Too much insistence can not be placed on this point. The use of homogeneous material is an indispensable prerequisite.

If the experiments are to contribute to the better understanding of the greater vegetation units the experiment stations will need to be critically located.

Probably the most promising field for experimentation at the present time is the investigation of the processes of vegetation. There are so many vague notions and dogmatic statements regarding the processes of competition, migration, adjustment, etc., in relation to the climatic factors, that the rewards for pioneer work will be ample. Here again the methods and materials must be carefully considered. In certain of these problems pedigreed (or better perhaps standardized) plants will give far more definite conclusions than those whose composition is unknown. In others, the more nearly we approach actual habitat conditions and investigate actual habitat processes, the more useful will be the results.

Experiments thus guarded may lead not only to a better understanding of vegetation, but they will also contribute to the science of evolution. If the methods used will bear inspection both from the standpoint of the process of heredity and from the processes of vegetation, natural selection and adaptation may be resolved into processes of more definite meaning.

The recognition of the importance of the results of ecological investigations in the practice of agriculture, horticulture and forestry has added much to their intrinsic interest. Some of the problems are perhaps beyond the reach of the individual worker. Fortunately there are several institutions in the United States within whose scope these problems lie. That they have already begun the publication of contributions to this field is the best evidence that both the larger and the smaller problems of the climatic relations of vegetation will be more adequately studied in the near future.

NOTES AND LITERATURE

RECENT EXPERIMENTS ON THE INHERITANCE OF COAT COLORS IN MICE

The domesticated varieties of rodents, rabbits, guinea-pigs, rats and mice, have furnished exceptionally favorable material for analyzing the facts of Mendelian inheritance. The simple formulæ that at first sufficed to explain the results have become more complex as the work has progressed until, at present, the situation has become not a little intricate owing to the different interpretations that the facts have received. This complication is, however, paralleled by progress in the study of plants, fowls, pigeons, sheep, swine, beetles, moths, snails, etc. Despite the elaboration that Mendel's originally simple law has undergone, it is significant how little there is in later discoveries that is believed to be incompatible *in principle* with this law, which may seem to vindicate itself in every direction where new facts come to light. This is nowhere better illustrated than in the latest facts and newest theories relating to inheritance of color in mice.

The earlier work of Allen, Darbishire, Davenport and Cuénot has given the relative order of dominance of the colors. These stand yellow (Y), gray (G), black (B), chocolate (Ch) and white (W). Each color is dominant to all that follow it in the order given and recessive to all that precede. Cuénot's results with white mice—albinos—showed that albinos stand in a class by themselves. White mice may carry *latent*[1] the factor for producing any color, although so long as white mice are mated, they produce only white. Cuénot's suggestion has been widely adopted, namely, that two factors are essential to produce any color; one of these is common to all colors and is called the color producer (C), the other is specific for each special color (Y, G, B or Ch). When C is absent, no color can arise, although the other factor, the determinant, may be present: hence white mice are characterized by the absence of the color producer (C)

[1] The term "latent" has come to have another significance in recent work. In general it now means the presence of one factor only when two are necessary for the development of a character.

although they carry one or more of the color determiners. In fact no white mice are known in which all determiners are absent, and from the nature of the case none could arise. An example may make this clearer. It is assumed that white mice first arose by the loss of the factor C. Suppose this occurred in a gray mouse, CG. It would then contain only the factor G and no C. For convenience the absence of C is represented by the letter A. It might appear that nothing—no symbol—would better represent this condition, but in practise it is convenient to indicate the absence of C; or in other words, to represent the paired character (negative here) of C. A, therefore, is the allelomorph of C, *i. e.*, C and A form a pair of contrasted characters. An example will again make this evident. A gray mouse CG crossed with an albino mouse AG, produces a colored mouse with the formula, CGAG. In the germ cells of this mouse the contrasted characters are $\frac{C}{A}$ and $\frac{G}{G}$, which give, as possible combinations, CG and AG. If we suppose two such mice, male and female, are paired, the possible unions of their germ cells may be represented thus:

A G	C G	
A G	C G	
AGAG	A G C G	
	A G C G	CG
1AGAG;	2AGCG;	1CGCG

The first term is a pure albino (extracted recessive); the second, a gray mouse carrying white recessive (a dominant recessive or heterozygote); the third term, a pure gray (extracted dominant). If the A's were omitted in the formula the outcome would be the same, but its presence is useful in arranging the contrasted characters in the germ cells; for, C always has A or C as its allelomorph, never G (or any other determiner). Hence the advantage of the symbol A. Failure to arrange the pairs of allelomorphs properly will give results incompatible with the theory.

In another graphic way the utility of representing an absent factor by some symbol can readily be shown. Suppose the characters are carried by certain material bodies in the egg—a purely preformation conception that dominates (or is latent in) all recent Mendelian speculation. If the color determiner is

carried by one body and the color producer by a different one, the pairs of allelomorphs will be $\frac{C}{C'}\ \frac{G}{G}$; every gray mouse carries these two pairs which separate at some time in the germ cells so that each germ cell (egg or sperm) carries one of each, C, G. Now an albino must arise by failure of a germ cell to contain C, the germ cell is simply 0 (zero) G, but since the same body that carried C may still be present (only one of its characters, namely C, being absent) the presence of that body is represented by A.

Let us now work out the case a step further. If this germ cell, AG, combines in fertilization with another germ cell, CG, of another individual, the resulting individual will be CGAG. The allelomorph pairs will be $\frac{C}{A}, \frac{G}{G}$. If such a mouse again pairs with a gray one, only gray mice will result. In time, however, enough mice of the formulæ CGAG will arise so that two such may meet; then and only then will an albino mouse *appear* amongst the gray offspring. Thus the conditions that produce the albino must arise two or more generations before the actual albino mouse is discovered.

This example shows, *on the theory*, how sports of this kind (recessive) that appear in nature are due to conditions that arise in the germ cells of an individual several generations earlier. The only possibility, on the theory, that such recessive sports could appear at once would be when several individuals changed in the same direction at the same time. Then the possibility of two germ cells of the same kind meeting would be realized. Recognizing the rarity of the appearance of sports, one may hesitate to assume that two such forms appear at the same time and pair with each other.

This view is based on the assumption that sports arise by the dropping out of one character in a germ cell. If the absent characters arise in some other way, after the germ cells have met for example, the situation is different, but the assumptions here made are in conformity with present-day development of Mendelian inheritance.

Our case was selected, however, not to illustrate how recessive sports arise and later appear, but to show how absent factors may be represented by bodies that in hybridizing become the partners of bodies containing that factor. Hence the supposed advantage of representing such absent factors by a definite

symbol standing for imaginary bodies; for such bodies, on this assumption, may carry other characters that remain, even though one be lost, and these other characters would still be subject to Mendelian rules and be associated with the absence of a character.

In the earlier work on mice and other forms the different colors, Y, G, B, Ch, W, are represented as allelomorphic pairs. Thus Y pairs with G, or G with B, or Y with Ch, etc. It follows, that if these color determiners are carried by definite bodies, these must always be the same kind of body or homologous bodies; otherwise they would not stand in this relation to each other. Thus a gray mouse paired with a chocolate would give a gray mouse, GCh whose germ cells would give the pair $\frac{G}{Ch}$. Two such mice paired would give:

G		Ch					
G		Ch					
G	G	G	Ch				
		G	Ch	Ch	Ch		
1	G G,	2	G Ch,	1	Ch Ch		

Similarly for every other combination. As a matter of fact gray by chocolate gives not only gray and chocolate but some black mice in the second generation. The formulæ fail to explain this result. Bateson, who was one of the first to point this out, was led therefore to a new formulation of the facts, and Cuénot to still another. Their views will be given later.

Another difficulty in connection with the inheritance of yellow was soon discovered by Cuénot. Yellow mice bred to yellow give not only yellow, but other colors as well. This would occur, of course, if the yellows were heterozygous. Thus YG by YCh would give yellows (YY, YG, YCh) and grays (CG). Some of the yellows should be YY, and two such paired should give only yellows. Cuénot was unable to produce such pure yellows. He therefore adopted a special explanation (selective fertilization) for this case. His view will come up again later.

A third complication arose in the case of dilute colors. In certain experiments, that need not be given here in detail, Cuénot found that the only assumption that would account for the facts was that two other factors—a strengthening or enforcing character (foncé) F, and a weakening or diluting factor

(dilué) D. The presence of F changes chocolate to black, the presence of D (in the absence of F) changes black to chocolate, and chocolate to dilute chocolate (or silver fawn).

In certain races of colored mice, the eyes are pink (absence of pigment) as in albinos. The presence of the factor that produces this condition has an effect on the coat color, according to Cuénot, hence he introduces a further set of factors that affect the color. By means of these several factors the inheritance in complex cases was explained.

It has been pointed out that in all gray rodents the color gray is due to a banded or barred condition of each hair. Each hair, in fact, contains bands of yellow, black and chocolate, arranged in definite sequence and in definite regions of limited extent. Hence gray is not a color in the sense that yellow or black or chocolate are colors, but is made up of all three. It is their arrangement that is the chief agent in producing gray animals. For this reason Castle has introduced a further factor, a barring or ticking factor instead of a gray factor. Hence gray is no longer allelomorphic to the other colors, but these colors are characterized by the absence of the barring factor and by the presence of one (or more) of the other colors.

Finally the hairs of black mice are known to contain chocolate pigment, so that black is not strictly allelomorphic to chocolate, although crossed with chocolate the Mendelian ratio for black and chocolate appears.

These and other discoveries show that the first representation of the pairs of characters will no longer suffice to account for the conditions that exist, although they give the Mendelian expectation for the cases first studied. We may next proceed to examine in more detail the hypotheses advanced to meet the more complex situation.

Bateson and his co-workers have discovered certain cases of inheritance which have led them to assume that *in crosses* the allelomorph of a given character is the absence of that character. For mice the following symbols are used:

CGB .....Gray or agouti
CgB .....Black
CGg .....Cinnamon agouti
Cgb .....Chocolate

So long as gray is bred to gray each character has its like for its allelomorph; $\frac{C}{C'}\ \frac{G}{G'}\ \frac{B}{B'}$. But each germ cell will contain only one C, one G, one B. Similarly for any other color bred to its like.

If gray (CGB) is bred to chocolate (Cgb) the resulting mouse has the composition CGBCgb. The allelomorphs are $\frac{C}{C'}\ \frac{G}{g'}\ \frac{B}{b}$. These hybrids bred together give the results shown in the next table. The possible germ cells of each will be CGB, CGb, CgB, Cgb, which by combination give the results here shown: 12 grays, 3 blacks, 1 chocolate.

CGB CGB gray	CGB CGb gray	CGB CgB gray	CGB Cgb gray
CGb CGB gray	CGb CGb gray	CGb CgB gray	CGb Cgb gray
CgB CGB gray	CgB CGb gray	CgB CgB black	CgB Cgb black
Cgb CGB gray	Cgb CGb gray	Cgb CgB black	Cgb Cgb chocolate

Thus the black mice that appear in this cross in the second generation are due to the absence of G and to the presence of the factor B. The single chocolate amongst the 16 mice is due to the absence of both G and B in the presence of C. Hence, Miss Durham recognizes chocolate (Ch) and color factor (C) as the same. Cuénot accounts for the results as follows. The gray mouse has the strengthening factor F along with C and G. The chocolate mouse has the diluting factor D along with C and Ch. The combination gives FCGDCh. The pairs are $\frac{F}{D'}\ \frac{C}{C'}\ \frac{G}{Ch'}$. Omitting C, present in all combinations, we find the possible combinations are FG, FCh, DG, DCh. Two such mice crossed give the kinds of offspring shown in table on page 500.

The results are 9 gray, 3 dilute gray, 3 black, 1 chocolate, and these are the actual numbers realized. The dilute grays are grays without black and are known as cinnamon agoutis. Whenever F occurs with Ch the combination gives black, whenever D occurs alone with Ch (once) the result is chocolate.

FG FG gray	FG FCh gray	FG DG gray	FG DCh gray
FCh FG gray	FCh FCh black	FCh DG gray	FCh DCh black
DG FG gray	DG FCh gray	DG DG gray	DG DCh gray
DCh FG gray	DCh FCh black	DCh DG gray	DCh DCh chocolate

Both hypotheses account for the numerical outcome. Some other criterion must decide between them. The criterion is found in the recent work of Miss Florence M. Durham who has pointed out that chocolate can not be dilute black, since a dilute form of black is known, which is quite different from chocolate.[2] Let us examine her results.

Black and chocolate are found either in a dense condition when the mouse is called black or chocolate, or in a dilute state, *i. e.*, with the pigment granules scattered. Dilute black is blue and dilute chocolate is silver fawn in the "fancy." Black dominates blue and chocolate dominates silver fawn on the older terminology. But it is known that black mice often contain chocolate whose presence is obscured by the darker color, black. This relation Bateson calls epistatic. In the same sense black is epistatic to blue; and chocolate is epistatic to silver fawn.

Black crossed with blue gives black only. Such heterozygous blacks inbred give 3 blacks to 1 blue. Similarly chocolate crossed with silver fawn gives chocolate. These inbred give 3 chocolate to 1 silver fawn.

The most interesting result reported by Durham, is seen when black, *i. e.*, blue, is crossed with chocolate. The result is black, because the chocolate supplies the strengthening factor and makes the dilute black dense black which is epistatic to chocolate.[3] In

[2] There may be two quite distinct meanings however attached to "dilute." Cuénot means the black pigment is changed to chocolate pigment. Durham means that the black pigment granules are sparse in the dilute form. See next footnote.

[3] This experiment shows that Durham's interpretation of the dilute color is correct; Cuénot's is incompatible with the experiment, unless the factor for Durham's dilute colors is different from the diluting factor of Cuénot.

the second generation such black mice give approximately

9 black, 3 blue, 3 chocolate, 1 silver fawn,

which is the Mendelian expectation.

When blues are mated to silver fawns the offspring are all blue. These inbred give three blues to 1 silver fawn.

Miss Durham's hypothesis gives a consistent account of the relation of the dense and dilute colors to each other.

The dilute colors are modified to some extent, as Cuénot first showed, by the condition of the eye color. Most mice with colored coats have black eyes. The black eye is due to black pigment in most cases, but in chocolates and in some yellows the dark eye is due to chocolate pigment, as Castle and Durham have independently found. A silver fawn with pink eyes may be of a different color from a silver fawn with dark eyes. How this modification results is not yet known. In fact, this relation of dilute colors to eye color offers a promising field for further inquiry.

An examination of the hair of dilute mice shows great differences in the amount of pigment in each hair and the color of the animal is modified by the average number of hairs of a given kind. A considerable range of shades is evident. Whether this is only a fluctuating character, or whether pure races of different shades can be made that give Mendelian proportions, if crossed, remains to be worked out. It is not entirely certain, I think, that the pigment granules themselves are not only scattered to varying degrees but may be even lighter or darker. Whether this is due only to size or to another factor is not yet known.

These dilute colors should combine with ticking to produce different shades of gray in addition to cinnamon agouti. Some of the grays that I have met with appear to fall under this head.[4] Whether the diluting factor for black and chocolate will act as a diluter for yellow is not known. Here we meet with a question of great importance in further study of the colors in mice.

In addition to albinos with pink eyes, white animals with black eyes are known to occur in many groups of animals. Such a race of fancy mice exists. Miss Durham reports that these white mice crossed with colored mice with uniform coats produce

[4] Thus cinnamon agouti crossed to silver fawn may produce in the second generation a pinkish agouti with light chocolate in place of dense chocolate.

in the first generation some spotted mice. This result I have also repeatedly obtained. It remains to be discovered what relation exists between the white of such mice and the white of common spotted mice, for in these the spotting disappears in the first generation. It appears that the white mice with black eyes are derived from spotted mice in which the spotting has been carried so far that pigment remains in the eyes alone. If these mice are only extremes of the spotted conditions the results seem to indicate that a recessive character has been changed to a partially dominant one. Perhaps one might say that physiologically it has become stronger. On the other hand, these black-eyed white mice may have arisen not from extremes of ordinary spotted mice but from a different relation between black and white. It is interesting, however, to note that in rats the recessive spotted coat also partially dominates in the first generation.

Cuénot has shown that ordinary spotted mice behave towards mice with uniform coats as a simple recessive, appearing in the second generation as 1 to 3. But I have found in practise that it is almost impossible to give an exact classification of the mice in the F_2 generation. In some individuals there may be only a small white tip to the tail, or only a few hairs may be white. Whether to classify such mice as dominant or recessive is largely arbitrary. White hairs not infrequently appear in mice that seem to be uniform in color. I find them quite abundant in wild black rats (*Mus rattus*). In man they appear in old age, and in horses when the skin is injured, etc. These considerations raise the question whether the problem may not after all be physiological, the result being due to the activity of the cells rather than to the absence of factors in the sense in which that term is ordinarily used in Mendelian hypotheses. If so, the entire result may be one of physiological activity rather than one of presence and absence of factors in a morphological sense.

The inheritance of the yellow color in mice has been a standing puzzle. Cuénot attempted to explain the facts on the assumption that a yellow bearing sperm can not fertilize an egg bearing this color, but can fertilize any other sort of egg. In other words selective fertilization takes place. Hence every yellow individual contains latent another color; it is yellow because yellow "dominates" (?) the other colors. But if selective fertilization can take place in regard to the individual characters

carried by the germ we introduce a conception entirely foreign to the whole Mendelian scheme. There is no evidence of selective fertilization *in this sense* known elsewhere and it seems a very questionable advantage to introduce the factor into the Mendelian process. The evidence that Cuénot brought forward in a second paper to show that selective fertilization takes place is open to criticism. He points out that since half the eggs can not be fertilized by half the sperm, there should be fewer young born when yellow is crossed with yellow than when yellow is crossed with any other color. His data show in fact a lower birth rate for yellow by yellow than when yellow is fertilized by other colors. Two objections to this argument may be advanced. First we must suppose that there are sufficient sperm present to fertilize the few eggs set free at each menstruation. Even if a yellow egg is not fertilized by a yellow sperm it should be fertilized by one of the other sperms. Second the fertility of the yellow mice is in my experience lower than that of other colors.

In order to avoid the hypothesis of selective fertilization and accepting Cuénot's statement that pure (homozygous) yellow mice do not exist, I suggested tentatively that the yellow-producing factor is not allelomorphic to the other colors, but that the germ cells of yellow mice are represented by the symbols Y(B), B(Y), to take a single example; in other words that yellow and the other color, black in this case, alternately dominate and recede. In this way the numerical results follow. I went so far as to suggest, as a theoretical possibility, that a similar mechanism might explain the alternate nature of the germ cells in all Mendelian cases and pointed out how this view could be tested. I have made one such test with entirely negative results, so that I think this interpretation must be abandoned.

An experiment that I made with yellow mice showed, however, that the yellow bearing germ cells of yellow mice do carry other color factors than yellow, and this result, which is not in harmony with Cuénot's assumption for the behavior of yellow color in the gametes, offers the possibility of a different explanation. I crossed a yellow mouse with a spotted black mouse of known ancestry—it carried black only. Some of the offspring were yellow. Two of these inbred gave yellows, blacks, chocolates and albinos. Obviously the yellow bearing germ cells

of the grandparent carried the chocolate determiner since this was known to be absent in the black grandparent. Hence the yellow germ cells transmit the determiners for other colors.

Cuénot has objected to this conclusion on the ground that the chocolate grandchild was due to a diluting factor carried by the yellow grandparent. This objection would be valid if chocolate is the dilute form of black, but Miss Durham has shown that the dilute form of black is not chocolate and that chocolate itself has also a dilute form. This relation I have also seen in my experiments. Furthermore had there been a diluting factor in my original yellow, of which there is no evidence, I should have obtained blues and silver fawns in some of the descendants that were inbred for some time but this is not the case.

It is probable therefore that the yellow color is not the allelomorph of the other colors but may be transmitted along with them. Its allelomorph would be in Bateson's sense the absence of yellow. Even this assumption fails however to show why pure yellows do not appear, and we must look still further for an explanation of the behavior of yellow in inheritance.

Castle has made some important suggestions that bear on this question. The gray coat of rabbits is due, according to his analysis to at least five distinct unit characters represented in the formula

U
|
A—C—B—E
|
I

C is the color producer; A is the factor for ticking; B stands for black; U for uniform (*i. e.*, not spotted) distribution of color; I is the intensifier or strengthener; and E a factor that governs the extension of black over the body. For a black rabbit the same formula holds with A left out. For a yellow rabbit E is replaced by R, a factor that stands for the absence of black. A sooty yellow rabbit is like the last with A absent.

It will be noticed that there is no factor in these formulæ for yellow, because yellow is assumed to be present in all these rabbits, but since it has never been *lost* its claim to be looked upon as a unit character is not established. Castle believes that yellow is always present if C is present. Yellow rabbits therefore differ from gray, as stated above in the absence of E (not

of B, black) by which is meant that black is prevented from developing except in the eyes and the skin of the extremities. How far further analysis will justify these conclusions is uncertain, but the interest of the hypothesis lies in the character of the attempted analysis, for the composition of races of different colors is no longer explained as the result of a single color determiner but as the outcome of a considerable number of such determiners. The more recent speculations in Mendelian inheritance show a strong tendency to follow this direction. It might be said that color depends on the absence of certain determiners rather than on the presence of a special one.

It does not appear that Castle's scheme for rabbits will apply to mice unless amended, for the relation of yellow to the other colors appears to be different, and there is no evidence to show that it is present in black or in chocolate.[5]

The most recent attempt to account for the heredity of yellow in mice is that of Hagerdoorn. He points out that there are several kinds of yellow mice, a conclusion familiar to every one that has bred the animals for certain individuals give only certain other colors than yellow in the offspring. I have examples of this in my own experiments. Moreover, one can determine what those other colors may be by crossing yellows with other colors and breeding together the yellow offspring. Hagerdoorn also assumes that, in some yellows at least, an inhibiting factor must be present. This point may seem not improbable[6] from the fact that two yellows may produce in addition to yellows, grays and blacks or chocolates. Since the parents carried the factors for these colors and since they did not appear their absence may be attributed to suppression. So far little exception can be taken to the view since it is in harmony with certain facts. But it is further assumed that the barring factor that determines the distribution of the pigments on the individual hairs is "composed of two factors, one of which is the modifying factor present in the 'dominant' strain of yellow rodents. Its action, we see, is a partial inhibiting of the two darker pigments whenever these are present with it in one zygote.[7] I therefore propose the name of 'inhibiting factor' for it." The other

[5] The grounds for this statement are given later in the case of mice.

[6] Unless yellow is formed by combination.

[7] As shown by the absence of black or chocolate in the yellow band of the hair.—T. H. M.

component of the barring factor is called the "marking factor." If the marking factor is present and not the barring, the mouse would be black. A black mouse therefore contains a yellow band but this can not be seen because the black and chocolate pigments obscure it. If this is correct one would expect to extract from a black mouse the yellow pigment by a solvent for yellow. I shall give below the evidence that negatives this conclusion.

Hagerdoorn also thinks that yellow may be due in some cases to the absence of all pigments but yellow. In such a case either the marking or the inhibiting factor may also be present without its presence being noticeable. The following six classes of yellow mice are recognized:

(*a*) Present black, chocolate and yellow plus inhibiting factor.
(*b*) Present chocolate and yellow plus inhibiting factor.
(*c*) Present yellow plus inhibiting factor plus marking.
(*d*) Present yellow plus inhibiting factor.
(*e*) Present yellow plus marking factor.
(*f*) Present yellow.

Hagerdoorn states that he has "proof" of the existence of five of these six groups. Group (c) alone has not yet been recognized. Moreover he obtained homozygous individuals of each of these groups. Homozygous individuals of the same group bred to each other produce pure yellow strains, that is, strains that never produce any other color than yellow. The reason that Cuénot and others never obtained pure yellow is due to the fact that they crossed yellows of different strains and under such circumstances mice of other colors will appear. In passing, however, it should be noted that in Hagerdoorn's classification of yellows if individuals of strains (a), (b), (d) and (f) were crossed only yellows should appear in the first and in all subsequent generations. Thus the chance of getting pure yellows is as four to two, and it does not seem probable with so much in favor of hitting upon these combinations that such strains would not have been obtained by Cuénot or Durham, who have studied the problem extensively.

Hagerdoorn's evidence in favor of his classification of yellow is obtained by crossing yellows, not with each other, but with mice of other colors or with albinos of known (?) composition. The pairings are too complicated to discuss here in detail and in the absence of numerical data, to show how often the results

cited occurred it would not be profitable to attempt to go further into the matter. One example alone of extreme importance may be cited. One yellow male mated to chocolate gave only chocolate young; the same male mated to black gave only black young. If the number of young is large enough to establish the case conclusively it is a distinct advance in our study of yellow mice. Hagerdoorn assumes that this yellow male contains yellow alone and that neither the barring nor the inhibiting factor is present. Hence the cross with black gives only black because the black obscures the yellow in the hair. Similarly for chocolate. If this is the correct interpretation as much yellow could be extracted from these hybrids as from a yellow mouse but this test was not made. The only other possible conclusion would be that not enough young were obtained to show that yellows were not produced by this pairing. We must await the publication of the numerical data. It should be added that the yellow male was tested by crossing with an albino strain possessing the barring factor and only yellow young appeared. This shows the absence of black or chocolate in the yellow, for were they present some gray mice should have appeared according to the hypothesis. Whatever discoveries the future has in store for us these experiments are of great interest, especially in so far as they point out a better method for studying yellows than any so far reported. The assumption that yellow pigment is present in black and chocolate can be readily tested. I have made such a test and find that black hairs put into caustic potash give no evidence of yellow to the extent that yellow exists in yellow hair as shown by the same solvent.[8] The fact that caustic potash also extracts chocolate to some extent complicates the result.

The hypothesis seems also to call for the presence of yellow pigment throughout the gray hair and not only in the yellow band. It is more difficult to test this view and observation would be of no avail since the yellow might be obscured by the presence of black or chocolate. It is a point of no small importance to remember that if an inhibiting factor combined with a marking factor gives the barred or ticked hair of gray mice these factors act at only a particular period in the formation of the hair by suppressing the development of black and chocolate, for the tip and the base of such a hair are dark. If mark-

[8] Whether some blacks exist without yellow is a further question not touched by this test.

ing here and elsewhere in animals is due to factors of the sort postulated they are controlled (?) by a periodic function of the hair bud. We meet here with the same problem the embryologist encounters in proportionate development or interrelation of the parts. Whether this is a dynamic *function* (epigenetic) or can be referred to a system of *factors* in the germ is a difficult problem and for the future to decide.

Before leaving this question of yellow mice a few well known facts may be stated. Yellows exist from a deep orange to a pale lemon yellow. All intermediate gradations may be found. Whether these are in reality a graduated series or a series of overlapping conditions we do not yet know. The presence of other pigments combined with yellow is also familiar to every student of these mice. If yellow is due to an inhibiting factor that factor must at times very imperfectly do its work of inhibiting. I have a race of sports of the house mouse with white bellies, gray backs and yellow sides. The hairs on the sides may be pure yellow, which should be due to the action of the inhibiting factor in this particular region only, since on the rest of the upper surface the hairs are ticked. Even in gray mice single hairs may be yellow.

In some yellow mice the belly is pure white. This must be due to a further factor that in this region inhibits the yellow, the yellow itself being the result of another inhibiting factor. In other words an inhibitor of yellow must also be postulated. It might be assumed of course that the white belly is due to the absence of yellow in the region, but since the mouse can produce yellow its absence in the belly must also be accounted for by some special assumption. Again we meet with the localization factor—a problem that Mendelian studies have scarcely yet approached except by the purest symbolic representations.

The fact that many rodents change the color of their hair according to age indicates that the physiological condition of the animal is an important factor in determining its color. If the mechanism of Mendelian inheritance involves only the shuffling of morphological determinants, as implied in many current conceptions of the mechanism of inheritance, the changes that take place in the same individual are difficult to understand unless it be admitted that temporal and local conditions affect the development of the determiners. Such an admission is practically equivalent to referring the development of a color,

for example, to the *extent* to which physiological (chemical) processes are carried out in an individual or part of an individual. Inheritance from this point of view would be a physiological process depending on an inherited degree of activity of the protoplasm (subject to local modifications) rather than the result of sorting out of morphological unities.

Since the preceding review and criticism was written an important paper by Oscar Riddle has appeared in which he takes the same position that I have done elsewhere[9] in regard to the process of Mendelian inheritance. He bases his criticisms on some facts concerning the changes that certain melanin colors undergo as the result of the stage of oxidation to which they are carried. If what happens outside the body furnishes any hint in regard to what takes place in the formation of color in animals and plants these facts rehearsed by Riddle are of great importance in relation to the inheritance of color-production. He writes:

> Here is then a *possible* picture of the basis of Mendelian segregation and proportion, but without recourse to hypothetical "particles" or to immutable and immortal factors. An apparently very specific end-result of an oxidation would be traceable in the germ only in the strength or pitch of a general vital process, and not at all in mnemons or representative particles packed with unthinkable precision, order and potentiality into (presumably) the chromosomes. . . The nature of present Mendelian interpretation and description inextricably commits to the "doctrine of particles" in the germ and elsewhere. It demands a "morphological basis" in the germ for the minutest phase (factor) of a definitive character. It is essentially a morphological conception with but a trace of functional feature. Although heredity is quite surely a functional process of major complexity, it may be recalled that the primary and fundamental Mendelian conception of this process utilizes not a single finding of the science of biochemistry, . . . With an eye seeing only *particles*, and a speech only symbolizing them, there is no such thing as the study of *process* possible. . . It has been possible, I think, to show by means of what we know of the genesis of these color characters that the Mendelian description—of color inheritance at least—has strayed very wide of the facts: it has put factors in the germ cells that it is now quite certainly our privilege

[9] See Chapter XXVII in my "Experimental Zoology," 1907, where the same problem is discussed in relation to Sex Inheritance; and in my paper "What are 'Factors' in Mendelian Explanations," read January 1909, before the American Breeders Association, Vol. V, 1909.

to remove; it has declared discontinuity where there is now proved continuity; it has postulated preformation where there is now evident epigenesis.

T. H. MORGAN.

LITERATURE CITED

Allen, G. M. Heredity of Coat Color in Mice. *Proc. Am. Acad. Art and Sci.*, XI, 1904.

Castle, W. E. Fifty Years of Darwinism. New York, 1909.

Castle, W. E. and Allen, G. M. The Heredity of Albinism. *Proc. Am. Acad. Arts and Sci.*, XXXVIII, 1903.

Cuénot, L. L' Hérédité de la Pigmentation ches les Souris. *Arch. de Zool. Exp. et Gen.*, 1902, 1903, 1905, 1907.

Darbishire, A. D. Note on the Results of Crossing Japanese Waltzing Mice with European Albino Races. *Biometrika*, 1902.

Davenport, C. B. Color Inheritance in Mice. *Science*, XIX, 1904.

Durham, F. M. A preliminary Account of the Inheritance of Coat Colors in Mice. Reports to the Evolution Committee, IV, 1908.

Hagedoorn, A. L. Inheritance of Yellow Color in Rodents. *Univ. of California Publications in Physiology*, March, 1909.

Morgan, T. H. The Assumed Purity of the Germ Cells in Mendelian Results. *Science*, XXII, 1905.

———. Some Experiments in Heredity in Mice. *Science*, XXVII, 1908.

———. What are "Factors" in Mendelian Explanations? American Breeders Association, V, 1909.

Riddle, O. Our Knowledge of Melanin Color Formation and its Bearing on the Mendelian Description of Heredity. *Biol. Bull.*, XVI, 1909.

SOME EXPERIMENTS IN BREEDING SLUGS

Certain large naked mollusca or slugs, common in Europe, are noted for their numerous and striking color-variations, some of which seem to be correlated with climatic conditions. Little has been known concerning the inheritance of these color-forms, but Mr. Walter E. Collinge has recently made some experiments in breeding two of the species, *Arion ater* (or *empiricorum*) and *A. subfuscus*. The results of this work are given in the *Journal of Conchology*, the short paper containing them being Mr. Collinge's address as president of the Conchological Society, delivered October 17, 1908. As the publication is available to few in this country, and the facts cited are very interesting, it seems worth while to abstract part of them.

Arion ater is a very large and handsome slug, of which the following color-varieties were used or appeared in the experiments:

(1) *ater*, pure black. I was not quite clear about the meaning

of the expression "typical," as used by Mr. Collinge, but in reply to my question, he writes that in every case it was "the pure black form, not *nigrescens* or *plumbea*."

(2) *castanea*, a brown variety.

(3) *rufa*, a red variety. The reddest forms occur on the continent of Europe. The above three have the body unicolorous, though the foot fringe may vary.

(4) *albolateralis*, with the back black and the sides white, the two colors sharply separated. A very handsome variety, of restricted range, especially common in Wales. Mr. Collinge writes me that the specimens he used were found in the vicinity of Birmingham.

(5) *scharffi*, like *albolateralis*, but the sides yellow instead of white.

In the first experiment, *castanea* was paired with *ater*, and the former laid 39 eggs, of which 24 were hatched and raised to maturity. These proved to be: 12 *ater* (with slight variations in foot fringe), 10 *rufa*, 2 *castanea*. From this lot, *rufa* was paired with *castanea*, and gave 14 in the next generation, of which four were *ater*, eight *rufa* and two *castanea*.

From the pairing of two of the eight *rufa*, fifteen slugs were raised, eight being *rufa*, two *ater*, and five subvarieties of *castanea*. (Mr. Collinge does not explicitly state eight *rufa*, but in a letter he confirms this interpretation of his account.) From the pairing of two *rufa* of the last generation sixteen adults were raised, twelve being *ater*, two subvarieties of *rufa*, and two subvarieties of *castanea*. Thus the experiment was carried to F_4, with results which are thoroughly Mendelian so far as the segregation of characters goes, but difficult to explain in regard to the appearance and proportions of the different kinds. It will be noted that *rufa* was twice chosen for breeding, to the exclusion of the other varieties, and the second time gave many more black slugs than the first. None of the bicolored forms appeared.

In a second experiment two *albolateralis* were paired, giving a progeny of 22 slugs, 20 being *ater* and 2 *scharffi*. This is so extraordinary that I asked Mr. Collinge particularly about it, and he confirms the result as stated. One would expect *albolateralis* to be homozygous, but the experiment shows that it is either heterozygous (in which case the proportions are hard to explain) or the results are incapable of explanation by any

ordinary hypothesis. I can not help suspecting that the parent slug had really paired earlier with a specimen of *ater*, the progeny in consequence not actually having the origin stated. In that case, supposing *ater* to be dominant, the results would not be so anomalous. It is not so easy to explain the results of the first experiment by the hypothesis of previous pairing, as in that, except for the original pair, the slugs were under observation from their birth.

Seeking a possible explanation of the *albolateralis* case, I consulted Dr. C. B. Davenport, who practically concurs with my view, writing: "The result of Collinge's mating is inexplicable to me except upon one or the other of two hypothesis; either that the parents were heterozygous or else, as you suggest, the supposed parents were not the actual ones, and one had previously paired with a black slug. Of course if *albolateralis* is a heterozygote, then striping is dominant as is usually the case and uniformity recessive. Uniform black would then be active in one quarter of the offspring, but the great proportion of pure black speaks against this hypothesis" (litt., March 22, 1909).

T. D. A. COCKERELL.

The Study of Stellar Evolution

An Account of Some Modern Methods of Astrophysical Research

By GEORGE ELLERY HALE

The introduction of photographic methods, the improvement of telescopes, and the rapidly increasing appreciation of the value to astronomy of physical instruments and processes, have revolutionized the observatory. From a simple observing station it has been transformed into a great physical laboratory, where images of the sun and stars are studied with many powerful instruments, and celestial phenomena are experimentally imitated with the aid of electric furnaces and other sources of intense heat. The result has been a great gain in our knowledge of the origin, development, and decay of stars. This books explains in a popular way how the life histories of the sun and stars are investigated. One hundred and four half-tone plates, made from the best astronomical negatives, place before the reader the most recent results of celestial photography in most of its phases.

250 pages, 104 plates, 8vo, cloth; net $4.00, postpaid $4.27

Address Dept. 38

THE UNIVERSITY OF CHICAGO PRESS

CHICAGO **NEW YORK**

Published in Europe by William Wesley and Son, 28 Essex Street, Strand, London, Price, 16s. 6d.

ESSAYS PHILOSOPHICAL AND PSYCHOLOGICAL.

IN HONOR OF WILLIAM JAMES, PROFESSOR IN HARVARD UNIVERSITY

BY HIS COLLEAGUES AT COLUMBIA UNIVERSITY

This volume is intended to mark in some degree its authors' sense of Professor James's memorable services in philosophy and psychology, the vitality he has added to those studies, and the encouragement that has flowed from him to colleagues without number. From Prefatory Note.

PHILOSOPHICAL ESSAYS.

The New Realism.....GEORGE STUART FULLERTON
Does Reality possess Practical Character?.....JOHN DEWEY
A Factor in the Genesis of Idealism.....WENDELL T. BUSH
Consciousness a Form of Energy.....WM. PEPPERRELL MONTAGUE
Perception and Epistemology.....FREDERICK J. E. WOODBRIDGE
Substitutionalism.....C. A. STRONG
World-Pictures.....WALTER BOUGHTON PITKIN
Naïve Realism: What Is It?.....DICKINSON S. MILLER
Kant and the English Platonists.....ARTHUR O. LOVEJOY
A Critique of Kant's Ethics.....FELIX ADLER
The Abuse of Abstraction in Ethics.....HERBERT GARDINER LORD
Purposive Consistency, the Outline of a Classification of Values.....G. A. TAWNEY
The Problem of Method in Mathematics and Philosophy.....HAROLD CHAPMAN BROWN

PSYCHOLOGICAL ESSAYS.

Pragmatism in Æsthetics.....KATE GORDON
The Consciousness of Relation.....R. S. WOODWORTH
On the Variability of Individual Judgment.....FREDERIC LYMAN WELLS
The Validity of Judgments of Character.....NAOMI NORSWORTHY
Reactions and Perceptions.....JAMES MCKEEN CATTELL
A Pragmatic Substitute for Free Will.....EDWARD L. THORNDIKE

With Photograph of PROFESSOR JAMES.

LONGMANS, GREEN & COMPANY. **91 Fifth Avenue, New York City**

The American Naturalist

A Monthly Journal, established in 1867, Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Organic Evolution and Heredity

CONTENTS OF THE FEBRUARY NUMBER

Charles Darwin and the Mutation Theory. CHARLES F. COX.

Juvenile Kelps and the Recapitulation Theory. II. Professor ROBERT F. GRIGGS.

Notes and Literature: *Plant Phylogeny*—The Origin of the Archegoniates, Dr. BRADLEY M. DAVIS. *Holothurians*—Clark's The Apodous Holothurians, W. K. FISHER. *Leeidoptera*—The Blue Butterflies of the Genus Celastrina, Professor T. D. A. COCKERELL. *Vertebrate Paleontology*—The Lysorophidæ; Stegocephala; The Cotylosauria; The Oldest Known Reptile; The Age of the Gaskohle; Bison Occidentalis; Nectosaurus; Callibrachion, Dr. ROY L. MOODIE. *Parasitology*—The Sleeping Sickness Bureau, Professor HENRY B. WARD. *Exploration*—Camp-fires on Desert and Lava, Dr. ROY L. MOODIE.

CONTENTS OF MARCH NUMBER

Invitation Papers at the Baltimore Meeting of the Botanical Society of America; Darwin Memorial Session:—
Darwin as a Naturalist; Darwin's Work on Cross Pollination in Plants. Professor WILLIAM TRELEASE.
Darwin's Influence upon Plant Geography and Ecology. Professor FREDERIC E. CLEMENTS.
Darwin's Work on Movement in Plants. Professor HERBERT MAULE RICHARDS.

An Examination of Darwin's "Origin of Species" in the Light of Recent Observations and Experiments. Professor EDWIN LINTON.

The Distinction between Development and Heredity in Inbreeding. Dr. EDWARD M. EAST.

Breeding Experiments with Rats. Professor T. H. MORGAN.

Shorter Articles and Discussion: The Chub and the Texas Horn Fly, Dr. ROY L. MOODIE. A New Camel from the Lower Miocene of Nebraska, HAROLD JAMES COOK.

Notes and Literature: *Heredity*—The Chondriosomes as Bearers of the Hereditary Qualities, F. PAYNE. Cultural Bed Mutations in the Potato.

CONTENTS OF THE APRIL NUMBER

Heredity of Hair Color in Man. GERTRUDE C. DAVENPORT and CHARLES C. DAVENPORT.

A Mechanism for Organic Correlation. Professor G. H. PARKER.

Recent Advances in the Study of Vascular Anatomy.
Vascular Anatomy and the Reproductive Structures. Professor JOHN M. COULTER.
The Progress of Plant Anatomy During the Last Decade. Professor EDWARD C. JEFFREY.

Shorter Articles and Correspondence: A Note on the Degree of Accuracy of the Biometric Constants, Dr. RAYMOND PEARL. Pure Strains as Artifacts of Breeding. O. F. COOK.

Notes and Literature: *Heredity*—The Nature of "Unit" Characters, Dr. W. J. SPILLMAN. *Environment*—Dr. FRANK E. LUTZ. *Experimental Zoology*—Hybridology and Gynandromorphism, Professor T. H. MORGAN. *Echinodermata*—Red Sea Crinoids, Dr. AUSTIN HOBART CLARK.

CONTENTS OF THE MAY NUMBER

The Categories of Variation. Professor S. J. HOLMES.

The General Entomological Ecology of the Indian Corn Plant. S. A. FORBES.

Notes and Literature: *Biometrics*—Some Recent Studies on Growth. Dr. RAYMOND PEARL. *Experimental Zoology*—Cuénot on the Honey Bee, Professor T. H. MORGAN. *The Upholding of Darwin*—Poulton and Plate on Evolution, V. L. K.

CONTENTS OF THE JUNE NUMBER

Heredity and Variation in the Simplest Organisms. Professor H. S. JENNINGS.

The Color Sense of the Honey Bee — Is Conspicuousness an Advantage to Flowers? JOHN H. LOVELL.

Variation in the Number of Seeds per Pod in the Broom, Cytisus scoparius. Doctor J. ARTHUR HARRIS.

Present Problems in Plant Ecology:
The Trend of Ecological Philosophy. Professor HENRY C. COWLES.
The Present Problems of Physiological Plant Ecology. Dr. BURTON LIVINGSTON.

Notes and Literature: Notes on Evolution, V. L. K. DeVries's Species and Varieties, Dr. GEORGE H. SHULL. *Embryology* — On the Totipotence of the First Two Blastomeres of the Frog's Egg. Dr. J. F. McCLENDON.

CONTENTS OF THE JULY NUMBER

Selection Index Numbers and their Use in Breeding. Dr. RAYMOND PEARL and FRANK M. SURFACE.

A Contribution to the Theory of Orthogenesis. Dr. ALEXANDER G. RUTHVEN.

The "Presence and Absence" Hypothesis. Dr. GEORGE HARRISON SHULL.

Present Problems in Plant Ecology: Vegetation and Altitude. Professor CHARLES H. SHAW.

Shorter Articles and Correspondence: Pleistocene Swamp Deposits in Virginia. Dr. EDWARD W. BERRY.

Notes and Literature: *Heredity*—A Case of Non-Mendelian Heredity. Dr. W. J. SPILLMAN.

Single Number 35 Cents **Yearly Subscription, $4.00**

The NATURALIST will be sent to new subscribers for four months for One Dollar

THE SCIENCE PRESS

Garrison, N. Y. **Sub-Station 84: NEW YORK** **Lancaster, Pa.**

VOL. XLIII, NO. 513 SEPTEMBER, 1909

THE AMERICAN NATURALIST

A MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

CONTENTS

Page

I. On an Early Tertiary Land-connection between North and South America. Dr. R. F. SCHARFF 513

II. Notes on the Relations of the Molluscan Fauna of the Peruvian Zoological Province. Dr. WILLIAM HEALEY DALL 532

III. Remarkable Development of Starfishes on the Northwest American Coast: Hybridism; Multiplicity of Rays; Teratology; Problems in Evolution; Geographical Distribution: Professor A. E. VERRILL 542

IV. Shorter Articles and Correspondence: Is there a Selective Elimination of Ovaries in the Fruiting of the Leguminosæ: Dr. R. HARRIS. 556

V. Notes and Literature: *Ichthyology*—Ichthyological Notes, President DAVID STARR JORDAN. *Parasitology*—Professor H. B. WARD. *Plant Cytology*—The Permanence of Chromosomes in Plant Cells, Dr. BRADLEY M. DAVIS . 560

THE SCIENCE PRESS

LANCASTER, PA. GARRISON, N. Y.

NEW YORK: SUB-STATION 84

The American Naturalist

MSS intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS

Lancaster, Pa. Garrison, N. Y.

NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

Important New Scientific Books

PUBLISHED BY THE MACMILLAN COMPANY

Botany

The Origin of a Land Flora. A Theory based upon the facts of Alternation. By F. O. BOWER, Sc.D., F.R.S. With numerous illustrations.

Cloth, gilt top, xi+727 pp., illus., index, 8vo, $5.50 net.

NOTE.—A profound study in the morphology of the lowest forms of plants, with special reference to the development of their reproductive systems. The author endeavors to show that the present land flora has originated from an aquatic ancestor, and traces the methods of specialization to the land habit, and the establishment of the forms of the higher plants. A book of the highest importance not only to botanists but to biologists in general.

NEW AND STANDARD HAND-BOOKS ON AGRICULTURE, ETC.

Elements of Agriculture, Southern and Western. By W. C. WELBORN, B S., M.S., M.P.A.

Cloth, xvi+329 pp., illus., appendix, glossary, index, 12mo, $.75 net.

NOTE.—This is a thoroughly modern treatise on farming as practiced in the Gulf States, from the point of view of the scientific agriculturist. It is adapted to school use, but is of practical service to any farmer in that part of the country. The author is vice-director of the Texas Experiment Station.

Re-issues of the highly valued Hand-Books known as the Garden Craft and Rural Science Series, edited by L. H. BAILEY, of Cornell University, Editor of "Cyclopedia of American Horticulture," "Cyclopedia of American Agriculture," etc.

The Principles of Fruit Growing. By L. H. BAILEY.
Tenth Edition, $1.50 net, by mail $1.66.

Irrigation and Drainage. By F. H. KING.
Fifth Edition, $1.50 net, by mail $1.68.

Principles of Vegetable Gardening. By L. H. BAILEY.
Sixth Edition, $1.50 net, by mail $1.68.

Bush Fruits. By FRED W. CARD.
Fourth Edition, $1.50 net, by mail $1.66.

Fertilizers. By EDWARD B. VOORHEES.
Tenth Edition, $1.25 net, by mail $1.38

Farm Poultry. By GEO. C. WATSON.
Sixth Edition, $1.25 net, by mail $1.42

Published By **The Macmillan Company** 64-66 5th Ave., New York

THE

AMERICAN NATURALIST

VOL. XLIII *September, 1909* No. 513

ON AN EARLY TERTIARY LAND-CONNECTION BETWEEN NORTH AND SOUTH AMERICA

R. F. SCHARFF, PH.D., B.SC.

NATIONAL MUSEUM OF IRELAND, DUBLIN

THAT the two great continents—North and South America—have only become joined to one another by land in later Tertiary times, is a widely accepted assumption. Yet the various authorities who have made this problem a subject of special investigation have not all come to precisely the same conclusions as to the geological age during which this union of the two continents was brought about.

A study of the marine fishes on both sides of the isthmus of Central America, for example, convinced Dr. Günther[1] that up to a recent geological period the latter was only represented by a chain of islands similar to that of the Antilles. But the number of species of fishes on the Atlantic and Pacific coasts of Central America that were supposed to be identical has been considerably reduced during more recent surveys. They no longer amount to more than 4.3 per cent. of the total number of fishes known to occur in both areas. Professor Jordan[2] on that account maintains that the isthmus has not been depressed during the lifetime of most of the existing species. The submergence, he argues, must have supervened at a more remote time. In the belief that the

[1] Günther, A. C. L. G., "Study of Fishes," p. 280.

[2] Jordan, D. S., "Study of Fishes," Vol. I, pp. 274–280.

Miocene may be taken as the date of origin of the modern genera of marine fishes, he contends that an open communication between the two oceans may have existed during that geological period. It is important to note that the sea currents seem at that time to have set westward, thus favoring the transfer of Atlantic rather than Pacific types across the isthmian area.

Mr. Regan[3] is inclined to put the date still a little further back in urging that the marine connection between the two oceans ceased to exist at the beginning of the Mioeene.

An investigation of the Crustacea and their distribution led Dr. Ortmann[4] to the conclusion that at the dawn of the Tertiary era an oceanic connection was in actual existence between the Atlantic and the Pacific in the isthmian region. This communication, he thinks, persisted until the Miocene. In the commencement of that period the isthmus was elevated, thus joining North and South America.

The Mexican amphibians and reptiles have been utilized by Dr. Gadow[5] in the solution of the same interesting problem with the result that he assumes the establishment of land-continuity between North and South America in either late Oligocene or early Miocene times.

The whole character of neotropical zoology, remarks Dr. Wallace,[6] whether as regards its deficiencies or its specialties, points to a long continuance of isolation of South America from the rest of the world, with a very few distant periods of union with the northern continent.

Geologists have discussed this subject mostly from paleontological evidence. Professor Gregory[7] clearly demonstrated that the idea of an interoceanic connection as late as the Pleistocene period, as suggested by Dr. Spencer,[7a] could no longer be entertained. In arriving

[3] Regan, C. T., "Fishes of Central America," p. xxx.
[4] Ortmann, A. E., "Geographical Distribution of Decapods," p. 359.
[5] Gadow, H., "Mexican Amphibians and Reptiles," p. 236.
[6] Wallace, A. R., "Distribution of Animals," Vol. II, p. 80.
[7] Gregory, J. W., "Palæontology of the West Indies," p. 305.
[7a] Spencer, J. W., "Reconstruction of an Antillean Continent," p. 134.

at a final decision as to the approximate date of orgin of the Central American land bridge, he was mainly influenced by Professor Scott's reference to the occurrence of Caryoderma a supposed glyptodont edentate in the Miocene Loup-Fork deposits. He urged, therefore, that the waterway across Central America was in all likelihood finally closed in the lower Miocene or possibly even in the upper Oligocene. As Caryoderma, however, is now believed to be a reptile and not an edentate, this argument no longer holds good.

Less definite are the results obtained by Dr. Hill[8] after a careful study of the rocks near the Isthmus of Panama. The only geological periods, he thinks, since the Mesozoic era, during which the Pacific and Atlantic Oceans could have been in communication with one another, would be the Eocene or Oligocene. It is important to note that Dr. Hill's conclusions were based entirely on his observations at the Isthmus of Panama. The geology of the remainder of Central America is as yet too imperfectly known to form the basis for similar speculations.

The most important pronouncement perhaps which has yet been made on the subject under discussion is that by Professor Osborn.[9] His intimate knowledge of the fossil terrestrial mammals of North America enabled him to affirm that North and South America were joined to one another more than once, as Wallace had suggested. The first union occurred in Mid-Cretaceous and perhaps early Tertiary times. Hereafter the continents separated once more until the Pliocene period.

Dr. Smith Woodward,[10] Mr. Lydekker and also Professor Depéret[11] hold similar views with regard to the more recent junction of the two continents.

The evidence on which Professor Osborn based his belief in the first and much earlier land connection between North and South America was unknown when Mr. Lydek-

[8] Hill, R. T., "Geological History of the Isthmus of Panama," p. 269.
[9] Osborn, H. F., "Mammalian Palæontology," p. 99.
[10] Woodward, A. S., "Palæontology," p. 429.
[11] Depéret, C., "Transformations of the Animal World," p. 282.

ker[12] wrote his work on the Geographical History of Mammals. He was under the impression, therefore, that the mammalian fauna of the South American region had been totally isolated from that of North America up to about the end of the Miocene. I shall shortly return to Professor Osborn's views as soon as I have completed my brief historical review of the first problem.

Professor Lapparent[13] concurs with Mr. Lydekker's opinion that the interchange of waters between the Atlantic and Pacific oceans across Central America could only have ceased to exist at quite the end of the Miocene period.

Finally, in his treatise on the development of continents, Dr. Arldt[14] maintains that the Central American land bridge must have originated at the commencement of the Pliocene period, and with this view I fully agree. Part of Central America no doubt had already risen above the ocean at a much earlier period, but in its present outlines and extent it must be regarded as a geologically recent development.

All those in fact who have seriously considered the problem, either from the standpoint of a marine or a terrestrial zoologist or from that of a paleontologist concur in the opinion that North and South America were separated from one another by a marine channel or by wide seas during part of the Teritary era. This, however, is the only point in which there is a general agreement. While some contend that the junction between the two continents had only been effected in comparatively recent geological times, others hold that within the life history of the great class of mammals, either in the early Tertiary or late in the Secondary era, a land bridge between North and South America had once before existed, by means of which an interchange of the faunas could have been brought about. It is this supposed earlier land connec-

[12] Lydekker, R., "Geographical History of Mammals," p. 119.

[13] Lapparent, A. de, "Traité de Géologie," p. 1318.

[14] Arldt, Th., "Entwicklung der Kontinente," p. 597.

tion and its probable nature and extent that I wish to discuss.

Dr. Wallace already vaguely indicated that there may have been several very distant periods of union in the past of the Southern with the Northern continent. This supposition received a startling confirmation by the discovery first by Dr. Wortmann and then by Professor Osborn[15] of true armadillo remains in the middle Eocene beds of Wyoming. If he does not actually speak of a direct land connection between the two continents in early Tertiary times, Professor Osborn[16] suggests as much in his remark that this discovery "adds another fact to the growing evidence that North and South America were related in the Mid-Cretaceous and perhaps early Tertiary and then separated again until the Pliocene." He does not specify in any way in what manner this relationship had been brought about. His views would be of particular interest, considering that Dr. von Ihering's extensive zoological and botanical researches have led him to believe that the South American continent itself must be of comparatively recent geological origin.

The latter declares that South America had arisen as a continent only since the Oligocene period. It then consisted of two parts united by a narrow strip of land in the west, which later on developed into the great mountain chain of the Andes. These two parts, which he calls "Archiplata" and "Archiguiana," were previously separated from one another. The first embraced Chile, Argentina, Uruguay and southern Brazil, the other the highland of Venezuela and Guiana. Each of these possessed, according to Dr. von Ihering,[17] its own characteristic fauna and flora and these were totally distinct from one another.

A somewhat similar theory as to the origin of South America, largely based on the geographical distribution of fresh-water decapods, has been advanced by Dr. Ort-

[15] Osborn, H. F., "An Armadillo from the Middle Eocene," pp. 163–165.
[16] Osborn, H. F., "Mammalian Palæontology," p. 99.
[17] Ihering, H. von, "Archhelenis and Archinotis," p. 79.

mann.[18] In place of the present Southern continent he thinks that toward the end of Mesozoic times, there existed the old Brazilian land (Archiplata), an Antillean continent (including the West Indies and Venezuela) and also the Chilean coast range. These three land masses were separated from one another by wide oceans. Just before the close of the Secondary era the Antillean continent, and with it Venezuela and even the Galapagos Islands, became united with western North America, the latter being then still detached from eastern North America. When Venezuela in early Tertiary times at last became fused with the other larger South American land masses, the interoceanic connection across Central America had severed it from North America.

Under such geographical conditions the Wyoming edentates alluded to by Professor Osborn could only have been derived from Venezuela, it being the sole portion of the present Southern continent that had any relationship with North America in those remote times. No fact, however, has been brought to light, either in the recent or fossil history of the edentates to lead us to imagine that they had originated in the northern part of South America.

That South America owes its origin to the union of several independent land masses is so clearly indicated by the existing fauna of the continent, that a similar evidence should also be revealed by a study of its rocks and fossils.

The geology of South America is unfortunately as yet little known. Yet even such a cautious observer as Professor Suess[19] ventured to suggest, on stratigraphical grounds, that an arm of the sea may have penetrated right across the continent in Cretaceous times. The archaic rocks of eastern Brazil and Guiana certainly were then raised above the sea, since the younger formations appear to be superimposed with great regularity further and further to the west of this ancient formation. Dr.

[18] Ortmann, A. E., "Geographical Distribution of Decapods," pp. 365–366.

[19] Suess, E., "Antlitz der Erde," Vol. II, p. 683.

Katzer[20] contends that during part of the Mesozoic era the Pacific ocean extended eastward to the shores of this land, whose rivers then drained westward into the ocean, as they even continued to do until Miocene times.

While it is therefore by no means evident from the geologist's point of view how and when the various land masses became joined to form the present South America, the geographical distribution of the living fauna, together with a study of the paleontology, has furnished most valuable hints as to the probable geological history of the continent.

Dr. Gill claims that the fishes are among the best indicators of former geographical conditions. Turning to the most recent studies on the South American fish fauna, those of Professor Eigenmann,[21] we find that he also is impressed by the dissimilar elements of which it is composed. He explains this varied character of the fauna by the supposition that two independent land masses, originally separated in the region of the Amazon valley, became welded together in early Tertiary times.

In his attempted restoration of the geographical conditions of South America during the Eocene period, Professor de Lapparent[22] depicts an aspect contrasting with that of other observers, and yet he recognizes a division of South America into two parts, for he represents the continent as being dissevered by a marine channel between the Rio Negro in Argentina and Southern Peru.

Of all the maps illustrating ancient distribution of land and water, that of Dr. Arldt[23] is the most striking in originality. He connects northern South America in late Cretaceous times by land with western Mexico, but not by way of Central America. He assumes that the latter was submerged at that time and that an independent land bridge extended from southwestern North America through the Galapagos Islands to Colombia. This north-

[20] Katzer, F., "Geologie des Amazonengebietes," p. 254.
[21] Eigenmann, C. H., "Fishes of South and Middle America," p. 528.
[22] Lapparent, A. de, "Traité de Géologie," p. 1455.
[23] Arldt, Th., "Entwicklung der Kontinente" (map 19).

ern complex of land was isolated from the southern part of South America by a wide sea channel stretching right across the continent.

His conception of an extensive land having once flourished to the west of Central America, while the latter was largely submerged, is not altogether new. In alluding to the east-westward trend of the Antillean Cordillera and its abrupt termination on the Pacific coast of Guatemala, Professor Suess[24] makes a suggestion as to its former westward prolongation. Precisely at the point, he says, where the arcuate continuation of this chain might be expected to meet the principal chains of South America, lie the volcanic Galapagos Islands.

Various indications in the structure of the Isthmus of Panama moreover left the impression on Dr. Hill's[25] mind that large areas now covered by the Pacific, to the west of the isthmus, were once replaced by an extensive land surface.

Nothing more, however, can be deduced from geological testimony as to the presence of any land connecting North and South America at a time when Central America may have been still wholly or partially submerged. Nor can we even surmise from these suggestions at what geological period such hypothetical land may have existed. Other methods will have to be employed in order to discover the manner by which the Eocene armadillos reached North America.

If we examine the whole eastern Pacific coast line from Alaska to Cape Horn, we notice that there are two areas that have apparently remained entirely unsubmerged since Jurassic times to the present day. One of these occupies part of western Mexico and Lower California, the other a strip of the southern coast line of Chile. It is the latter coast cordillera which Dr. Burckhardt[26] believed to be the remaining remnant of a mighty Pacific continent, because porphyritic conglomerates of Cretaceous age are heaped

[24] Suess, E., "Antlitz der Erde," Vol. II, p. 263.
[25] Hill, R. T., "Geology of the Isthmus of Panama," p. 217.
[26] Burckhardt, C., "Traces géologiques d'un continent," pp. 12–14.

against its eastern flank, whereas still further east the latter grade into fine-grained rocks, thus indicating that the land from which they were derived lay westward, out in the ocean.

While we need not here dwell upon the theory of a former Pacific continent[27] so ably supported by Professor Haug on purely geological grounds and by Professor Hutton on zoogeographical data, I should like to draw attention to some features in the geographical distribution of animals and plants which prove that southwestern North America and southwestern South America are intimately related to one another in their fauna and flora. This relationship can not be explained as the product of a similarity in soil and climatic conditions. It is not a case of mere convergence. It can be shown that it already existed in the distant past, and I venture to think that this relationship implies the presence of a former direct land connection between these two ancient areas, when the continent of South America was still in the making.

It was Dr. Wallace[28] who first directed attention to the remarkable fact that many genera of insects from the north temperate regions reappeared in temperate South America, being generally absent in the intermediate stations. He explained this phenomenon by the supposition that the northern forms had traveled southward during successive glacial epochs when the mountain range of the Isthmus of Panama might have become adapted for their advance in that direction. Their southward passage was believed to have been facilitated by storms and hurricanes which carried the insects across unsuitable territories.

This interpretation of a striking feature of geographical distribution seems to have been considered satisfactory at the time. At any rate no one has raised any protest so far as I am aware. Yet I am not at all disposed to admit its correctness.

[27] More detailed information on the theories relating to an ancient Pacific continent will be published in my work on the geological history of the American fauna.

[28] Wallace, A. R., "Distribution of Animals." Vol. II, pp. 45–47.

Let us take, for example, the case of Carabus, a genus of running beetles so familiar to North American entomologists. They are by no means easily transported to great distances by gales and hurricanes as Dr. Wallace avers, for the simple reason that these beetles can not fly. Their wing cases are permanently soldered together, and being generally found under clods of earth or beneath stones, the action of winds can have no appreciable influence on their dispersion. They are typical inhabitants of the northern hemisphere, being abundant in Europe, northern Asia and North America. A single species occurs in western Mexico. No Carabus has ever been taken in Central America or in the northern or middle states of South America. Yet in Chile and spreading into Argentina, no less than eleven species have been observed. For a distance of about fifty degrees of latitude the running beetles of the genus Carabus are quite absent and then reappear further south in numbers. Those entomologists, like Mr. Born,[29] who have made a special study of the Carabidæ, consider them eminently fitted for the purpose of demonstrating former changes of land and water.

Of the northern genera of butterflies Colias, Lycæna and Argynnis, which occur in Chile, the presumption, at any rate is admissible that they might have been transported to these far distant southern latitudes by accidental or occasional means of dispersal, such as those suggested by Dr. Wallace. Yet the case of the ant Lasius, a northern genus, which reappears in Chile, is more difficult of explanation on such an hypothesis.

We can not say of any of these invertebrates that they are confined to western Mexico in North America, though this appears to be the most southerly point on the northern continent where they occur. On the other hand the primitive earthworm Kerria is only known from Lower California and from the southern part of South America in Chile and Argentina. From the latter country it seems to have spread into Paraguay and southern Brazil.

[29] Born, Paul, "Zoogeographisch-Carabologische Studien."

Of particular importance is the ancient genus of land molluses Bulimulus. It is quite peculiar to America. Its nearest relation appears to be the Melanesian Placostylus. Bulimulus, which is almost characteristic of the west coast of America, is now divided into three great groups, one of which has its headquarters in Chile and Peru, the second is met with on the Galapagos Islands, Central America and the West Indies, the third is confined to Lower California and Mexico. These three groups are very similar in appearance, but Dr. Pilsbry[39] maintains that this resemblance, which is particularly noticeable between the Mexican and Chilean forms, is not so much a proof of close relationship as the result of similar environment. At any rate we notice here three distinct and discontinuous centers of radiation, two of which are situated on very ancient land surfaces, while the third mostly occupies islands whose origin certainly dates back to early Tertiary times.

Probably a still more ancient invertebrate is the curious Peripatus, an archaic arthropod with an extremely discontinuous distribution. Three distinct groups inhabit America. One of these is confined to southern Chile, another seems to have spread northward along the Andes from a Chilean center as far as Ecuador. At a distance of twenty degrees of latitude north of this northern outpost it reappears in western Mexico, while in Central America lives a third and perfectly distinct group which has spread thence to the West Indies and eastern South America.

In its three distinct centers of distribution all along the west coast of America it bears a certain resemblance to the range of Bulimulus just alluded to. The range is certainly suggestive of a very ancient and more direct communication than obtains at present between western Mexico and Chile.

The flora of the new world retains far more pronounced traces of that curious relationship between the southwestern areas of its two continents. The plants of both Chile

[39] Pilsbry, H. A., "Manual of Conchology," Vol. X, p. 127.

and southwestern North America, moreover, are better known than are the animals. Whatever may be the cause, not only is there a resemblance between families and genera in the two areas; the general similarity of the landscape and especially the occurrence in both of a profusion of cactuses strikes the casual observer at once. Many specimens of northern plants recur in identical forms in those distant regions of South America.

Professor Asa Gray[31] and Sir Joseph Hooker long ago directed attention to this very remarkable phenomenon.

More recently, Professor Engler[32] and Professor Bray have emphasized this affinity and speculated on the problems connected with it. The flora of the Rocky Mountains including the Sierra Nevada Mountains above the transition zone, and the mountains far to the south of them, though separated from one another by a stretch of some ten degrees of latitude of moist tropical country, abound in northern genera of plants such as Ranunculus, Anemone, Geranium, Spiræa, Geum, Rubus, Saxifraga, Vaccinium, Gentiana, Hieracium and others. The greater number of forms occurring in the southern continent are endemic, pointing to long-continued isolation. Yet certain species, even of the Rocky Mountain Arctic alpine region, reappear in the extra-tropical Andes towards the southern extremity of South America, being, so far as is known, wholly absent from the Mexican mountains as well as the tropical Andes. Among these Professor Bray mentions particularly *Gentiana prostrata*, *Trisetum subspicatum*, *Primula farinosa* and its variety *magellanica*, *Draba incana*, *Alopecurus alpinus*, *Saxifraga cespitosa*, *Polemonium microcanthum* and *Collomia gracilis*.

The lower Sonoran elements of plant life are likewise represented in the extreme south. *Orythea dendroidea*, *Chorizanthe commissuralis* and *Lastarriæa chilensis*, for example, do not occur in the vast regions that separate

[31] Gray, A., and J. Hooker, "Vegetation d. Rocky Mountain Gebietes," p. 292.

[32] Engler, A., "Entwicklungsgeschichte d. Florengebietes," Vol. II, p. 256.

the two areas. A few of these plants may possibly have been casually introduced from the one to the other. But Professor Bray[33] expresses the opinion that in most cases we have to deal with forms which were connected by a remote ancestry, and which flourished at a time and under conditions which permitted a more general distribution.

What these conditions were like he does not venture to inform us, but it must be evident that this flora is much older than the Pleistocene, during which time it has been supposed that the climatic conditions may have favored a southerly advance of northern forms. Specific changes, among certain plants as well as among some animals, seem to proceed with extreme slowness. We have the example of the still living redwood tree (*Sequoia sempervirens*) which has persisted unchanged since Mesozoic times, for the fossil *Sequoia Langsdorfi* is now considered identical with the modern form.

It appears to me possible, therefore, that the well-known and extremely discontinuous range of some of the alpine plants may be interpreted by the assumption that, like Sequoia, they are of vast antiquity and that they have spread along a continuous mountain chain which once extended in a direct line from southwestern North America to western Chile, before the Andes had risen from the floor of the ocean.

We know that a similar relationship between North America and southern South America prevailed already in Mid-Cretaceous times. No less than seventy-five per cent. of the plant remains recently discovered in a Mid-Cretaceous plant-bearing layer in Argentina are characteristic types of the Dakota-group flora.

Commenting on this discovery, Mr. Berry[34] dwells on the remarkable agreement of this southern flora with that developed in Mid-Cretaceous times in western North America. He urges that it certainly points to a community of origin. In these ancient South American deposits all the familiar northern genera Liriodendron,

[33] Bray, W. L., "Relations of the North American Flora," pp. 709–716.

[34] Berry, E. W., "Mid-Cretaceous Geography," p. 510.

Liquidambar, Cinnamomum and Sassafras are met with. Even Platanus, Populus, Quercus and others are represented. No wonder that Mr. Berry[34] came to the conclusion that a geographical connection must have existed between North and South America during Mid-Cretaceous times. He thought that the plants referred to had spread southward from the north, while Professor Osborn favors the view that his Eocene Armadillo had advanced from the south.

Before concluding this short review on the evidences pointing to an early Tertiary direct land bridge between the southwestern portions of North and South America, a few observations on the paleontology of Patagonia and Chile may somewhat elucidate this interesting problem.

Edentates occur in the oldest Tertiary deposits of Patagonia or even pre-Tertiary, if Dr. Florentino Ameghino[35] is correct in assigning a Mesozoic age to the latter. The position which this savant has taken up and so courageously defended has been almost universally assailed. Professor Ameghino still holds that the now famous fossiliferous strata of Santa Cruz, which have yielded such a surprisingly rich harvest of mammalian remains are of Eocene age, while the likewise terrestrial Notostylops beds belong to the Cretaceous series.

The great majority of geologists, on the other hand, are of opinion that the Santa Cruzian deposits belong to the Miocene and the Notostylops beds to the Eocene period.

These beds are separated by marine strata which have been carefully investigated by the members of the Princeton Expedition to Patagonia. The invertebrates collected were described by Dr. Ortmann,[36] who considered them as certainly of Miocene age. He thus concurs in the opinion arrived at independently by the many eminent paleontologists, that both the terrestrial deposits above alluded to, the Notostylops and Santa Cruzian beds, are of Tertiary age.

[35] Ameghino, Flo., "Formations sédimentaires de Patagonie."

[36] Ortmann, A. E., "Princeton Expedition," p. 288.

To all appearances the question was finally settled when Dr. von Ihering[37] again challenged the results obtained by Dr. Ortmann, pointing out certain discrepancies in his determinations. Dr. von Ihering now maintains that only 4.9 per cent. of the species from the Santa Cruz marine beds are still living and, as the formation moreover corresponds to those of Oamaru in New Zealand and of eastern Australia, now generally included in the Eocene, he feels no hesitation in placing the Patagonian marine beds in the latter series. He, therefore, entirely supports Dr. Fl. Ameghino's latest views as to the Eocene age of these strata.

If Dr. von Ihering's conclusions are substantiated, and his arguments appear to me convincing, the more recent terrestrial Santa Cruzian deposit must be either of Oligocene, or as Dr. Ameghino believes, of Upper Eocene age.

Let us for a moment consider the geographical conditions in early Tertiary times of that region of South America in which these beds are found. The similarity in character of the Patagonian marine fauna on the east coast with the Tertiary of northern Chile on the west coast of the continent implies the existence of a connection between the two oceans. This supposition is further strengthened by the fact that eight per cent. of the eastern or Patagonian species of marine mollusca are found in the western Tertiary beds of Navidad in Chile.

Since a number of northern types of molluses make their appearance in the upper divisions of the Patagonian beds, Dr. von Ihering suggests that the supposed old land connection between Brazil and Africa had at that time been ruptured, thus opening a way for an invasion of the northern fauna. I have not previously alluded to this land bridge, Ihering's southern Atlantis or Archhelenis, because I am not dealing with this problem at present. It is not necessary, however, to conclude from the presence of northern molluses in the upper Patagonian marine beds that this supposed land bridge had broken down

[37] Ihering, H. von, "Mollusques fossiles de l'Argentine," p. 95.

completely in upper Eocene times. They could just as well have come from the Pacific, which seems to have freely communicated with the Atlantic across Patagonia. Not only are these northern invaders present in the Chilean deposits on the Pacific coast, there are many genera in the latter according to Dr. von Ihering,[38] such as Conus, Purpura, Oliva, Cassis, Cypræa and Littorina which never penetrated as far east as Patagonia at all. They thus denote the manner of dispersal of all the northern forms from north to south, and it appears as if they had gradually crept southward along some ancient coast line. But since there is no reason to suppose that the present Pacific coast of South America had come into existence already in early Tertiary times, we may assume that the ancient coast line lay farther west.

Down to Miocene times the influence of the Caribbean and even the European marine fauna continued to be felt on the Pacific side of South America. Dr. Ortmann[39] tells us that the north Peruvian Miocene fauna shows close affinities with the faunas alluded to. Several observers remarked on the circumstance that when Central America was submerged in early Tertiary times, the Caribbean and Atlantic species generally seemed to be drawn towards the Pacific by a strong current. We have noticed that the effects of this current in carrying northern Atlantic forms are traceable in the Tertiary deposits all along the Pacific coast of South America as far south as northern Chile and even on the Atlantic side of the continent in Patagonia, which then freely communicated by a marine channel with the Pacific.

On the other hand, the Tertiary molluses of Chile and California are very distinct from one another. This apparently implies that a barrier was interposed between the northern coasts of California or rather between the main portion of the Pacific coast line of North America and that of South America. Hence it tends to support my argument, that western Mexico and part of lower

[38] Ihering, H. von, "Mollusques fossiles de l'Argentine," p. 514.

[39] Ortmann, A. E., "Tertiary Invertebrates of Santa Cruz," p. 320.

California had a direct land comection with Chile. Dr. von Ihering[40] suggests that the Antillean arc which is continued to Guatemala and there abruptly terminates on the Pacific coast may have been continued westward in early Tertiary times in a great peninsula comprising the Galapagos and Sandwich Islands. He applied the term "Pacila" to it.

My reason for preferring to connect western Mexico and Chile in the manner I conceived, rather than adopt Dr. von Ihering's proposal, is that the spreading of Caribbean and Atlantic shallow water forms of molluses indicates a continuous shore line running north and south.

The Pacific coast of South America as it appears today had not yet emerged in early Tertiary times. The Andes were only just beginning to make their appearance. They must have risen as a series of islands parallel to the ancient coast that lay out in the west.

I picture to myself southern Chile as forming the extreme apex of a long penisula extending southward from western Mexico. Sometime during the Eocene period it became disconnected from Patagonia. The long peninsula was subsequently more and more reduced in size until only high mountains, such as the volcanic cones of the Galapagos Islands, remained above water. The peculiar lizards belonging to the genera Amblyrhynchus and Conolophus inhabiting these islands have their nearest relation in Phymaturus, which is confined to Chile, and not as we might expect to the much less distant Peru, Ecuador or Colombia. As long as any parts of the peninsula remained above water and attached to Mexico, it may have added its mammalian fauna to that of North America.

In such a manner it may possibly have come to pass that the northern genus of porcupine Erethizon is, according to Professor Scott, more like the fossil Steiromys from the Santa Cruz beds than the latter is to any of the South American porcupines. Steiromys, as Professor

[40] Ihering, H. von, "Archhelenis und Archinotis," p. 318.

Scott[41] informs us, is only a little more primitive than Erethizon, the change from the one to the other involving but a slight modification.

Erethizon is unknown in North America from pre-Pleistocene deposits, but there is no reason to assume that it had not originated long before the Pleistocene period. South American types of mammals may have existed in western North America from early Tertiary times onward without having left their remains in the more ancient deposits.

The theory of the former existence of a great lobe of land connecting western North America with southern South America during the beginning of the Tertiary era, while Central America and northern South America were still largely submerged is sustained by many facts in the geographical distribution of plants and animals. It seems to me to explain the undoubted affinities prevailing in the two areas in a better manner than by any other hypothesis. Against it may be urged that it is an unwarranted supposition to assume that existing species of plants can have preserved their specific characters since the Eocene period. Still we must not forget that one plant at least, *Sequoia sempervirens*, has lived without any appreciable change down to the present time from those remote ages. And even if we altogether eliminate the testimony elicited from a botanical source, there still remain zoological factors of importance as buttresses of the hypothetical bridge I have constructed.

May, 1909.

BIBLIOGRAPHY

Ameghino, Florentino. Les formations sédimentaires du Cretacé supérieur et du Tertiaire de Patagonie. *Anal. Mus. Nacional de Buenos Aires* (3 sér.), Vol. 8, 1906.

Arldt, Th. Die Entwicklung der Kontinente und ihrer Lebewelt. Leipzig, 1907.

Berry, E. W. A Note on Mid-Cretaceous Geography. *Science* (N. S.), Vol. XXIII, 1906.

Born, P. Zoogeographisch-Carabologische Studien. *Entomol. Wochenblatt*, Vol. XXV, 1908.

[41] Scott, W. H., "Mammalia of Santa Cruz," p. 417.

Bray, W. L. The Relations of the North American Flora to that of South America. *Science* (N. S.), Vol. XII, 1900.

Burckhardt, C. Traces géologiques d'un ancien Continent pacifique. *Revista do Museo de la Plata*, Vol. 10, 1900.

Depéret, Ch. The Transformations of the Animal World. (Intern. Scient. Series.) London, 1909.

Eigenmann, C. H. The Fresh-water Fishes of South and Middle America. *Popular Science Monthly*, 1906.

Engler, A. Versuch einer Entwicklungsgeschichte des Extratropischen Florengebietes. Leipzig, 1879–1882.

Gadow, H. The Distribution of Mexican Amphibians and Reptiles. *Proc. Zool. Society*, London, Vol. 2, 1905.

Gregory, J. W. Contribution to the Palaeontology and Physical Geology of the West Indies. *Quart. Journal Geol. Soc.*, Vol. 51, 1895.

Gray, A., and J. Hooker. Die Vegetation des Rocky Mountain Gebietes und ein Vergleich derselben mit der anderer Welttheile. *Engler's Botanische Jahrbücher*, Vol. 2, 1882.

Günther, A. C. L. G. An Introduction to the Study of Fishes. Edinburgh, 1880.

Hill, R. T. The Geological History of the Isthmus of Panama. *Bull. Mus. Comp. Zoology*, Harvard, Vol. 28, 1898.

Ihering, H. von. Archhelenis und Archinotis. Leipzig, 1907.

———. Les mollusques fossiles du Tertiaire et du Crétacé supérieur de l'Argentine. *Anal. Mus. Nac. Buenos Aires*, Vol. 14, 1907.

Jordan, D. S. A Guide to the Study of Fishes, Vol. I. Westminster, 1905.

Katzer, F. Grundzüge der Geologie des unteren Amazonengebietes. Leipzig, 1903.

Lapparent, A. de. Traité de Géologie, 4e éd. Paris, 1900.

Lydekker, R. A Geographical History of Mammals. Cambridge, 1896.

Ortmann, A. E. The Geographical Distribution of Fresh-water Decapods and its Bearing upon Ancient Geography. *Proc. Amer. Philos. Soc.*, Vol. 41, 1902.

———. Tertiary Invertebrates. Report Princeton Univ. Exped. to Patagonia, Vol. IV.

Osborn, H. F. An Armadillo from the Middle Eocene (Bridger) of North America. *Bull. Amer. Mus. Nat. Hist.*, Vol. XX, 1904.

———. Ten Years' Progress in the Mammalian Palaeontology of North America. *Comptes Rendus sixième Congrès intern. de Zoologie*, Berne, 1904.

Pilsbry, H. A. Manual of Conchology, Vol. X, 1895–96.

Regan, C. T. Biologia Centrali Americana. Pisces. 1906–08.

Suess, E. Das Antlitz der Erde. Wien. 1892–1901.

Scott, W. H. Mammalia of the Santa Cruz Beds. Report Princeton Exped. to Patagonia, Vol. V, 1903–05.

Spencer, J. W. Reconstruction of the Antillean Continent. *Bull. Geol. Soc. America*, Vol. 6, 1895.

Wallace, A. R. The Geographical Distribution of Animals. London, 1876.

Woodward, A. S. Outlines of Vertebrate Palaeontology. Cambridge, 1898.

NOTES ON THE RELATIONS OF THE MOLLUSCAN FAUNA OF THE PERUVIAN ZOOLOGICAL PROVINCE

DR. WILLIAM HEALEY DALL
SMITHSONIAN INSTITUTION

HAVING recently summarized the faunal relations existing between the mollusca of the deep sea, off the western coast of South America, and those of other regions,[1] it has happened that in reporting on a collection of mollusca submitted for examination by the government of Peru, it fell to me to compile a census of the mollusca inhabiting the shallow waters and coasts of the region known as the Peruvian zoological province. Such an enumeration had not been made for something like half a century. The much fuller knowledge of these animals now possessed by scientific students makes the number of species belonging to this region much greater than was formerly supposed, and modifies in consequence the conclusions formerly arrived at.

The littoral fauna has practically nothing in common with that of the abysses. The relations of the two groups of animals to each other, to adjacent faunas, and to the Tertiary fauna, have recently assumed a special interest, from the discussions by von Ihering and others as to the routes of Tertiary migrations.

It was thought therefore that a summary of the results deduced from a study of this faunal list would have a certain general interest not only for malacologists but for the students of historical geology.

The littoral marine molluscan faunas of the west coast of the two Americas, excluding the Arctic and Antarctic faunas properly so-called, were recognized more than

[1] *Bull. Mus. Comp. Zool.*, XLIII, No. 6, pp. 207–211, 1908.

half a century ago in their main outlines by Woodward.[2] They comprise, beginning at the north:

1. *The Oregonian Province*, extending from the limit of floating ice in Bering Sea south to Point Conception, Cal.

2. *The Californian Province*, ranging from Point Conception south to Lower California.

3. *The Panamic Province*, from Lower California including the Gulf of California, south to the Bay of Guayaquil, Ecuador.

4. *The Peruvian Province*, extending from Guayaquil south to the vicinity of the island of Chiloë in southern Chile.

5. *The Magellanic Province*, from Chiloë to the Fuegian Archipelago, and for a short but undetermined distance north on the Argentine coast, on the Atlantic side.

These provinces will eventually be recognized as containing minor divisions, with which, on this occasion, we are not concerned.

The distribution recognized in the term province appears to be directly dependent on the temperature of the surface stratum of the sea, which, in its turn, is distributed by ocean currents. In the case of the Peruvian Province a branch of the eastward-flowing South Pacific current diverges from the main stream and impinges upon the coast of South America in the vicinity of Chiloë Island. Thence it follows the coast northward, until by the northwesterly trend of the Peruvian shores it is diverted, in the vicinity of Point Aguja and Cape Blanco, to the westward, where it continues in the direction of the Galapagos group of islands. This current, known as the Peruvian or Humboldt current, throughout its entire extent maintains a temperature (varying with the season) of from 65° to 70° Fahrenheit. The temperature of the surface off Aguja Point, Peru, in November, was 65° F. The temperature of the water in the Magellanic Province in mid-summer varies from 50° F. in the straits themselves, to 55° F. on the Chilean coast in the vicinity of Valdivia.

[2] "Man. of the Mollusca," pp. 373–377, 1856.

The surface temperatures of the Peruvian current, as related to those of the Magellanic water, are therefore warmer; and, as compared with the Panamic waters, markedly colder. Precisely such a relation to the coast of North America is held by the southerly branch of the North Pacific current, which reaches the coast near Sitka with a summer temperature of 65° to 68°. This has diminished in the latitude of San Francisco Bay to 54 °F., but the current continues until in the vicinity of Point Conception, California, it is diverted off shore in a manner entirely analogous to the fate of the Peruvian current at Point Aguja.

The water of the Panamic Province is less disturbed by currents, receives the full heat of the tropical sun, and, as shown by Professor Alexander Agassiz, emerges from the Gulf of Panama, follows the coast toward Cape San Lorenzo, and is there diverted off shore toward the Galapagos Islands. Trees from the mainland with leaves still adhering to them are occasionally cast upon the shores of the Galapagos, as observed by Professor Agassiz; showing clearly that the current is not only present but has no inconsiderable motion. The temperature of this water near the coast of Ecuador and only a few miles from the limit of the Peruvian current, in November, varied from 70° to 83° F., and in March and April from 78° to 85° F. Among the Galapagos Islands the range in April was 81° to 83° F.

It will be noticed therefore that the currents fully account for the peculiarities of the Galapagos mollusk-fauna, which exhibits large contributions from the Panamic and Peruvian faunas with only a very unimportant tincture of the Indo Pacific in its make-up.

A series of surface temperatures measured in November at right angles to the Peruvian current off Point Aguja, by the U. S. S. *Albatross*, began with a temperature of 65° F. close in shore, rose quickly to 69° and later to 70° in the middle of the current, and declined again to 69° F. on its western edge.

The first exploration of the molluscan fauna of the Peruvian Province which was systematically carried on, was that of Hugh Cuming. He was resident for some years at Valparaiso, later dredged and collected vigorously at various points of the Bay of Guayaquil. Tradition has handed down the account that a severe earthquake (referred to by Darwin in the Voyage of the *Beagle*) laid bare a long stretch of coast where the shore mollusks, elevated above their natural situs, were accessible to the collector by the thousand. Mr. Cuming collected largely, and on his return to England these collections gave an opportunity to the systematic naturalists to describe many new Peruvian and Chilian shells. This lasted for a good many years. Broderip, Sowerby, Swainson, Gaskoin, Powys, Deshayes and Reeve worked on these collections during the first half of the nineteenth century. According to Woodward[3] Mr. Cuming's collection embraced 222 species from the coast of Peru, south of Paita, and 172 species from the coast then politically included in Chile. Of these probably half were common to the northern and southern portions of the province. A little later the explorations of Humboldt and Bonpland added a few species; the majority of their collection, it would seem, was not worked up.

M. Alcide D'Orbigny's South American investigations seem to have been, so far as this province is concerned, largely restricted to the Chilean portion of it. He collected 160 species, one half of which were common to Chile and Peru, while only one species was common to Callao and Paita. The inference naturally drawn from this last fact by Woodward and others was that the northern border of the province lay between those two ports. But this conclusion was due to imperfect knowledge, and is completely refuted by later information. At present more than 200 species are known to be common to Paita and Callao.

D'Orbigny's report with its atlas of fine illustrations

[3] Manual, p. 376.

is a classic source for information, relating, however, to South America as a whole rather than to the Peruvian Province.

Collections made by Gay and others, worked up in his monographic Historia de Chile, by Hupé, form the third large and well-illustrated contribution to the malacology of the province, chiefly restricted of course to the southern or Chilean portion.

The last important contributor to a knowledge of this fauna in these earlier days was the German naturalist Philippi, who added numerous species and useful illustrations in the *Zeitschrift für Malakozoölogie*, his "Abbildungen," and his "Atacama Reise."

Of course many minor contributors to the work, such as Lesson, Jonas, etc., might be mentioned, but I propose in this hasty sketch to touch only on the most important. The list of Tschudi's collection, ostensibly from Peru, as described by Troschel unfortunately contains numerous exotic Indo Pacific and Panamic species, so that its authority is seriously impaired. More recently the researches of Ludwig Plate, the Princess of Bavaria and others, have added essentially to our knowledge.

In considering the distribution of species along the coast of the province it should not be forgotten that the collections have not been made with equal thoroughness on different parts of the coast. The ports of Guayaquil, Paita, Callao and Valparaiso have naturally been much more thoroughly explored than any of the rest, and the careful collecting which would obtain the smaller species is not recorded to have been done at all, anywhere.

Dredging also is practicable with difficulty, except in the sheltered harbors which occur so rarely on this coast, or by the aid of a large steamer which could be had only under Government auspices on account of the great expense involved.

The small lots of material derived from the mud which came up on the anchor of the *Albatross* at one or two points, show that proper exploration will certainly reveal

the presence of many small species new or extralimital which are at present unknown. In determining what species should be included in the list I have depended somewhat upon the known characteristics, as regards distribution, of the groups to which the species belong. For instance, if I found a species reported from Guayaquil and belonging to a widely distributed group such as the Pholadidæ, though not actually reported from a Peruvian locality, I have not hesitated to include it, knowing that in all probability it will be found on more thorough search in Peruvian territory. There can be little doubt that a large number of the more mobile of the Panamic species reaching the Bay of Guayaquil will be found to have extended their range more or less within the northern border of the Peruvian Province; just as a certain number of the characteristic Magellanic species have traveled beyond their strict limits and mingle with the southern members of the Peruvian fauna. Species properly belonging to the Panamic Province and not reported as far south as Guayaquil or the Galapagos Islands, have been omitted from the list.

It will be observed that the list contains only a few minute shells. Doubtless these exist, and will be found when carefully sought for, but, as previously indicated, the majority of collectors seem to have confined their attention to the more conspicuous species.

I have included a certain number of pelagic forms, cephalopods, pteropods and nudibranchs, which are not strictly littoral, but are found occasionally thrown on the beaches or are captured within a short distance of the shore.

In any first census of this kind, some species will be included which later investigation will exclude. I have rejected a number of Tschudi's species as obviously exotic, but a small number remain which are doubtful, and which are indicated as needing confirmation. I have also omitted a few names which seemed to be almost certainly due to misidentification or to a confusion between such

localities as Arica and Africa. "Lumping" closely related species, such as some of the Siphonarias, has led certain authors to include purely Atlantic forms with their Pacific analogues under one name. So far as time, and the access to specimens, permitted I have tried to disentangle such cases and use only the name definitely belonging to the Pacific form. In making her dredgings the U. S. Fish Commission steamer *Albatross* seems to have avoided shallow water; and in the case of Dentalium, which has a wide range in depth, I have included a few species actually dredged beyond the 100 fathom line, but which will in all probability be found within it when sought for. No other deep-water species, however, has been admitted. An account of them will be found in my *Albatross* Report of 1908. In scanning the list those unfamiliar with the repetition of names so prevalent in Spanish geographical nomenclature will need to remember that there is a Tumbes in Chile as well as in Peru, and be on the look out for analogous cases. Species of Auriculidæ which are exclusively littoral, although pulmonate, have been included, also the salt-water Cyrenas, my aim being to include all species which are to be found along the shores of the province on the beaches and in the adjacent waters of the sea. Whatever deductions from the list may be necessary hereafter, I am convinced that they will be more than made up for by future additions from the ranks of the minuter species.

It is probable, though not by any means certain, that when we eliminate the overflow from the Panamic and Magellanic Provinces, the remaining fauna on this long stretch of coast may be susceptible of division into subfaunas, but it is too early to speculate about this possible feature of the distribution.

I have indicated in the preceding remark, the nature of the reservations which must be made in discussing the statistics of our present census of the Peruvian Fauna, and subject to those reservations we may now proceed to consider the figures.

The total number of species appears to be 869, of which 64 are pelagic and may be omitted from consideration in the matter of distribution, leaving 805. Taking the present political limits of the two countries as a starting point, we find seventy-one species reported from Peru exclusively, and one hundred and three restricted to Chile. But, as political and biologic boundaries rarely have anything in common, these data are not especially significant. We have 174 species restricted to Peru or Chile and 141 common to Peru and Chile, making 315 species proper to the Province itself. In addition to these we have 253 species common to the Panamic Province and to Peru, and 239 species of the Panamic Province which are known to reach the northern border of the Peruvian Province at or near Cape Blanco, many of which will doubtless be found to have a more extended southerly range. In addition to these there are 25 species whose range extends from Upper California south to Peru or even to Valparaiso.

At the southern extreme of the Peruvian Province it receives 41 recruits from the Magellanic Province, few of which range north of Valparaiso. Of the whole 805 species enumerated which are not pelagic, only 24 are known from the West Indies or Atlantic Ocean, most of which are Pholads, borers, or limpets; forms peculiarly liable to transportation long distances on ships or floating timber. The only species which can be regarded as also Indo-Pacific, are even fewer in number and to be included in the same category.

Eliminating all the pelagic species and all the Panamic species not shown to be now actually domiciled within the limits of the Peruvian Province, we have a population for and province of 566 species of littoral marine mollusks.

In Bulletin 84, of the U. S. Geological Survey, pages 25 28, 1892, I have shown that the average population for a warm temperate area (when the temperature ranges from 60° to 70° F.) is about 500 species of shell-bearing mollusks. Adding the species of nudibranchs, naked

tectibranchs and littoral cephalopods enumerated in our list, it would seem that the average is pretty well maintained in the case of the Peruvian Province.

Dismissing the minuter species from consideration as insufficiently known, the more striking characteristics of the Peruvian fauna may be summed up as follows:

1. There is an unusual proportion of the species which are black or blackish or of a lurid tint. This feature of the fauna has attracted attention from all who have studied it, and has been discussed by von Martens. It is particularly marked among the zoophagous groups.

2. The fauna is notable for its Fissurellidæ and Acmæidæ, its trochids of the genus Tegula, its numerous and peculiar chitons, its numerous cancellarias, the development of Calyptræidæ, of species of Arcidæ and of Thais, Chione, Semele, Petricola, Mulinia, all represented by numerous species.

3. The deficiencies in the fauna are as marked as the redundancies. There are notably few pectens or Lucinas, and the Tellinidæ are poorly represented. Acteon, the smaller tectibranchs, Conus, the Turritidæ especially, the Marginellidæ, Fusimus and its allies, Epitonium (Scala) and the Pyramidellidæ are all very poorly represented. Calliostoma and Margarita, Haliotis and Pleurotomaria are absent or barely represented.

The notion that the mournful colors of so many of the species might be correlated with the huge beds of kelp characteristic of these shores, seems to be negatived by the fact that in California similar kelp-beds afford a shelter to some of the most brightly colored Trochidæ, etc., and that, as I am informed by Mr. Coker, red and green seaweeds are abundant on the rocks below low-water mark, on a large part of the coast of Peru, and presumably also of Chile. This and a number of other problems await the investigators of the future.

Lastly, a survey of the characteristic groups of which the fauna is largely made up leads to the conclusion that the fauna is chiefly of southern origin. In spite of the

fact that many species are common to the Panamic fauna and a relatively small number to the Magellanic fauna, the more conspicuous types, like the blackish species of Tegula, have a Magellanic rather than a tropical character. This particular group has extended its range to Alaska on the north, and Japan on the northwest, but its metropolis is in southern Chile. The type represented by the various species of Thais and Acanthina has traveled the same road, and so has the Protothaca group of Veneridæ.

If we may accept as the original metropolis of a special type of mollusk that region where it is developed in the greatest number and variety of species and perhaps also with the most extreme limits of size and ornamentation, we shall have for example Buccinum and Chrysodomus focused in the boreal Pacific region; certain types of Thais and Acanthina in the region of southern Chile. Cook has called attention to the relation between *Thais lapillus* and the Oregonian *T. lamellosa*, and other species in the tropics of the Panamic and Antillean region; but viewed from an eastern Pacific standpoint the relatively few Atlantic forms may easily have originated in the Pacific where their existing representatives show a much more luxuriant development. There is only one Thais of the nucella type in the north Atlantic, but the north Pacific has five or six. It is very remarkable that in the Peruvian Province we have not a single distinctively old-world type of Mollusk. Those which seem to be such are really cosmopolitan types more familiar to us from old-world localities, perhaps, but not necessarily of old-world origin.

REMARKABLE DEVELOPMENT OF STARFISHES ON THE NORTHWEST AMERICAN COAST; HYBRIDISM; MULTIPLICITY OF RAYS; TERATOLOGY; PROBLEMS IN EVOLUTION; GEOGRAPHICAL DISTRIBUTION

PROFESSOR A. E. VERRILL

YALE UNIVERSITY

No other part of the world, of similar extent, so far as known, has so many species of shallow water and littoral starfishes as the coasts of Alaska and British Columbia, including Puget Sound. Many of the species range from San Francisco to the Aleutian Islands, but the most favored region is from Puget Sound to southern Alaska.

The forms known to me, including those from arctic Alaska, are about eighty species, besides fifteen named varieties. No doubt special physical conditions there have favored the remarkable development of this group, as well as certain other groups, on that coast.[1]

The entire region has a very broken coast line, innumerable islands, bays, fiords and straits, giving a great extent of sheltered coast line, bathed in pure sea-water and swept by strong tidal currents, all of which are very favorable to littoral marine life, vegetable as well as animal, thus providing an abundance of food for carnivorous forms, like the starfishes, most of which feed principally on mollusks.

These favorable conditions are notably shown by the great abundance of individuals as well as species, and also by the great size that many of the species attain. At least eight of the species of Asterias and allies become there over two feet in diameter.[2]

[1] Among other groups having a similar remarkable development on that coast are the Polyplacophora (Chitons), limpets, nemerteans, tubicolous annelids (Sabellidæ), etc.

[2] Among these very large species are *Asterias columbiana* Ver., *A. Troschelii* (St.) var. *rudis* V., *A. forcipulata* Ver., *Pisaster ochraceus* (Br.),

Perhaps the relative uniformity of the temperature during the entire year is one of the most important factors in determining, or permitting, the great abundance of life on this coast, just as it is in the deep sea. Although the water is cold, it is not subject to great extremes of heat and cold, like those of the eastern coast of North America. The rapid tidal currents have a powerful effect in preventing extremes of temperature, by constantly mixing the deeper water with the shallow.

But the nature of the starfish fauna and that of other groups, like the chitons, forces us to conclude that similar favorable conditions have existed on that coast continuously for several geological periods, and that no great extermination of marine life occurred there, even during the glacial period.

A number of the genera and higher groups are peculiar to that coast; others have there a remarkable development in number and variety of species, showing that their evolution must have gone along continuously for vast periods of time. In many cases primitive and highly specialized species of a family are associated. Therefore, that coast offers unusually favorable conditions for studying the evolution of the genera and species, having there their chief development. We should naturally expect to find still surviving there, representatives of some of the comparatively early or primitive species, associated with those of more modern origin, of the same groups. Such appears to be the actual condition in many instances.

However, the complete elucidation of these questions will require a large amount of careful investigation and very extensive collections.[3]

P. granulosus (St.), *P. Lutkeni* (St.), *P. papulosus* Ver., *Pycnopodia helianthoides* St. Also *Asterias acanthostoma* sp. nov., allied to *Troschelii*, but with long proximal adambulacral spines; dorsal spines small, acute, reticulated; proximally in transverse combs; rays very long.

[3] The collections that I have personally studied are large, but not always as complete as desirable. They are from the Canada Geological Survey, the Provincial Museum of British Columbia, Washington State University, Yale University Museum, U. S. National Museum, Harriman Alaska Expedition and others.

HYBRIDISM

One difficulty in these studies arises from the fact that certain of the species, usually very distinct, seem to hybridize in localities where their ranges overlap and the breeding seasons are coincident. Owing to the small variations in temperature the breeding season of most species is probably unusually prolonged, and this affords better opportunities for hybridization. Among such apparent hybrids, I will mention particularly those between *Asterias epichlora*, a small, usually six-rayed, diplacanthid species, and *Pisaster ochraceus* (fig. 7), a large, coarse, five-rayed, monacanthid species. The latter ranges from San Diego, Cal., to middle Alaska, and is one of the most abundant littoral species. The former ranges from Puget Sound to the Aleutian Islands. At Sitka and adjacent regions, on rocky shores, it is one of the very abundant littoral species. Although normally six-rayed, five-rayed specimens are common. It is one of those species that have the habit of carrying the eggs and young attached in clusters around the mouth.

From Sitka, Wrangel, etc., I have had a considerable number of specimens that appear to be true hybrids between these two very diverse species. They generally have the small size and form of *epichlora*, but some have the reticulated and nodular arrangement of the dorsal spines of *ochraceus*. And what is still more striking, several of them, looking like true *epichlora*, have more or less of the huge, sessile, dentate, dermal pedicellariæ (fig. 7) characteristic of *ochraceus* and the other species of Pisaster.

I have named six marked varieties of *epichlora*, which do not seem to depend on hybridization; or at least I could not satisfy myself of it. But those that I consider hybrids do not conform to any of the determinate varieties. However, it is easy to understand that if hybrids occur, as I believe they do, between *A. epichlora* and *A. hexactis*, which are much more closely allied and also occur commonly together, it would not be easy to determine the

fact. The same would be true in the case of hybrids between either of the latter and *A. Troschelii*, another commonly associated species at Sitka, etc. For although the latter is a large, five-rayed species, with long rays, when young it often closely resembles some varieties of *epichlora*. Therefore it is not very unlikely that some of the so-called varieties of the latter may also be hybrids. More extensive collections with minute comparisons can alone determine such questions.

The number of species of starfishes on that coast of the family Asteriidæ (usually referred to the genus Asterias), known to me is forty, with twelve named varieties. With so many species, many of them with overlapping ranges, numerous hybrids are likely to occur. The same remarks would, most likely, apply to certain groups of mollusks, annelids, etc., in which large numbers of species occur together.

Multiplicity of Rays

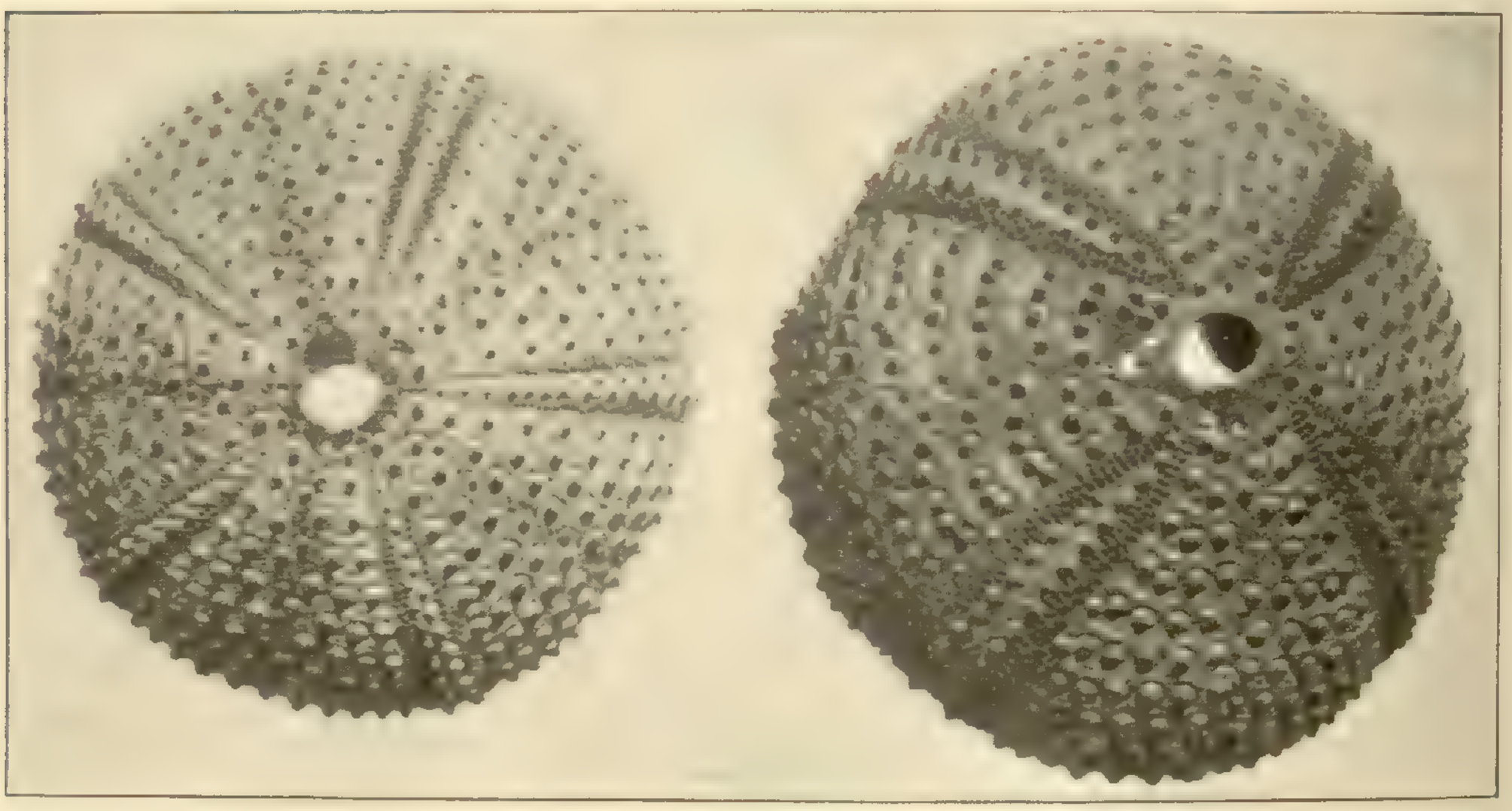
So far as known to me, no other region can be compared with the northwest coast, in respect to multiplicity of rays. It is particularly noticeable in the Asteriidæ, a family that is generally five-rayed in all other parts of the world, though there are many exceptions.[4]

On the northeast coast of America there are only two exceptions: *Asterias polaris*, with six rays (Labrador and northward), and *Stephanasterias albula*, with six to nine rays, and autotomous; (from New England northward). Of the forty northwest American species of Asterias and Pisaster, twelve, or thirty per cent., have normally six rays.[5]

Besides these, the remarkable related genus, *Pycnopodia*, is peculiar to that coast. Its single species, *P. heli-*

[4] It is also noteworthy that the genus Heliaster with several species, having from twenty four to fifty or more rays, is peculiar to the Pacific coast of America (Lower California to Peru). The record of one species from Hawaiian waters is probably an error.

[5] Among these are *Pisaster giganteus* (St.), *A. polythela* Ver., *A. hexactis* (St.), *A. æqualis* (St.), *A. epichlora* (Br.), *A. polaris* var. *acervata* (St.), *A. macropora* Ver., *A. Katherinæ* Gray, *A. dubia* Ver. = *A. Katherinæ* Per., *non* Gray.



a *b*

FIG. 1.—*Arbacia æquituberculata; a,* normal form; *b,* quadriradial specimen.

anthoides, which ranges from California to middle Alaska (Yakutat, etc.), has, when adult, twenty to twenty-four rays. It begins life as a five-rayed or six-rayed star, but acquires new rays, by budding in new rays, a pair at a time, symmetrically and side by side in succession.[6] This process is not known to occur in any other starfish, except in Labidiaster, which is an Antarctic genus of the family Brisingidæ. Several peculiar Antarctic starfishes seem to be allied to north Pacific forms.

But even those species of Asterias, etc., that are ordinarily five-rayed, occur not very rarely with six rays,[7] and the six-rayed species may occur with five rays (see note, teratology). In other families the same peculiarity is

[6] See Professor W. E. Ritter and G. R. Crocker (*Proc. Washington Acad. Sci.*, Vol. II, pp. 247–274, 1900), who give a good account of the process. I have observed many examples like theirs, but have also studied some in which there were five primary rays, and a few in which some new rays were produced, also, at irregular places, but this is unusual.

[7] I have recently collected many specimens of the very common five rayed New England species, *A. Forbesii*, near New Haven, Conn., which have four rays and six rays, and some that have seven, eight and even nine rays, by examining many thousands. About 1 in 2,000 has six rays; 1 in about 3,000 is four-rayed; 1 in about 10,000 is seven- or eight-rayed, at this time and place. Some of those with more than six rays may be due to complete repairs of injuries received in early life, with development of extra rays. (See H. I. King, "Regeneration in *Asterias vulgaris*," *Arch. Entwickel. Organ.*, IX, pp. 724–730, 1900). But this is evidently not the case with most of the four-rayed and six-rayed instances.

noticeable. Thus the peculiar genus Pteraster, which carries its young in a dorsal marsupial pouch, is found all around the world, rather sparingly, and with one exception[8] all the known species have until now, been five-rayed. The very young, taken from the pouch, agree in number of rays with the mother. On the northwest coast six shallow-water species are known, besides an additional allied genus.[9] One of these (*P. octaster* Ver.) has eight rays; another six rays.

Of Solaster, five shallow-water species are known. Of these, one (*S. constellatus* Ver.) seems to have, normally, but eight rays, an unusual number in the genus. The others have from nine to thirteen rays, the number varying in each species.

Teratology

Besides the species that normally have an increased number of rays, or vary indefinitely, there are others which have, more or less rarely, a smaller or larger number, as monstrosities. I propose to mention here a few such cases. Various other monstrous variations occur somewhat frequently, such as forked rays, supernumerary rays arising from the dorsal surface, etc. But these will mostly be discussed elsewhere.

The common large *Asterina miniata*, which ranges from south of San Francisco, Cal., to middle Alaska, becomes 175 mm. in diameter. It is normally five-rayed, but I have studied more than a dozen six rayed specimens (fig. 2), which are regular and normal in all other respects; some are of full size; most of the large six rayed ones were collected at Ocean Grove, Ore., by Professor W. R. Coe. In the same lot was one four-rayed specimen, 135 mm. in diameter. It is a little irregular, the greater part of one ray having been reproduced, but not to full size.

[8] *Pteraster* (*Heraster*) *obscurus* (Per.) = *Tenuaster borealis* Ver., has normally six rays (rarely seven). It is from Newfoundland Banks and Arctic ocean. Two other shallow water species occur on the New England coast, both five-rayed.

[9] This genus *Pterasteroides* Ver. nov. is proposed for *P. aporus* Ludwig. It is peculiar in having no dorsal osculum and in having spines around the central nephridial pore that do not reach the marsupial dorsal membrane.

Dermasterias imbricata is a common five-rayed or pentagonal species, but we have one regular, six-rayed, young specimen from Sitka. The majority of our specimens have numerous large bivalve and trivalve pedicellariæ in rows, below, and smaller ones dorsally, though most writers describe it as destitute of pedicellariæ. A regular six-rayed *Henricia læviuscula* from Alaska occurred, and also a six-rayed *H. sanguinolenta* var. *pectinata* from Bering Sea.

Solaster Stimpsoni Ver. = *Crossaster vancouverensis* De Loriol, 1897. One specimen of this species from British Columbia has one of the rays forked below, near the mouth, thus producing ten regular rays as seen from

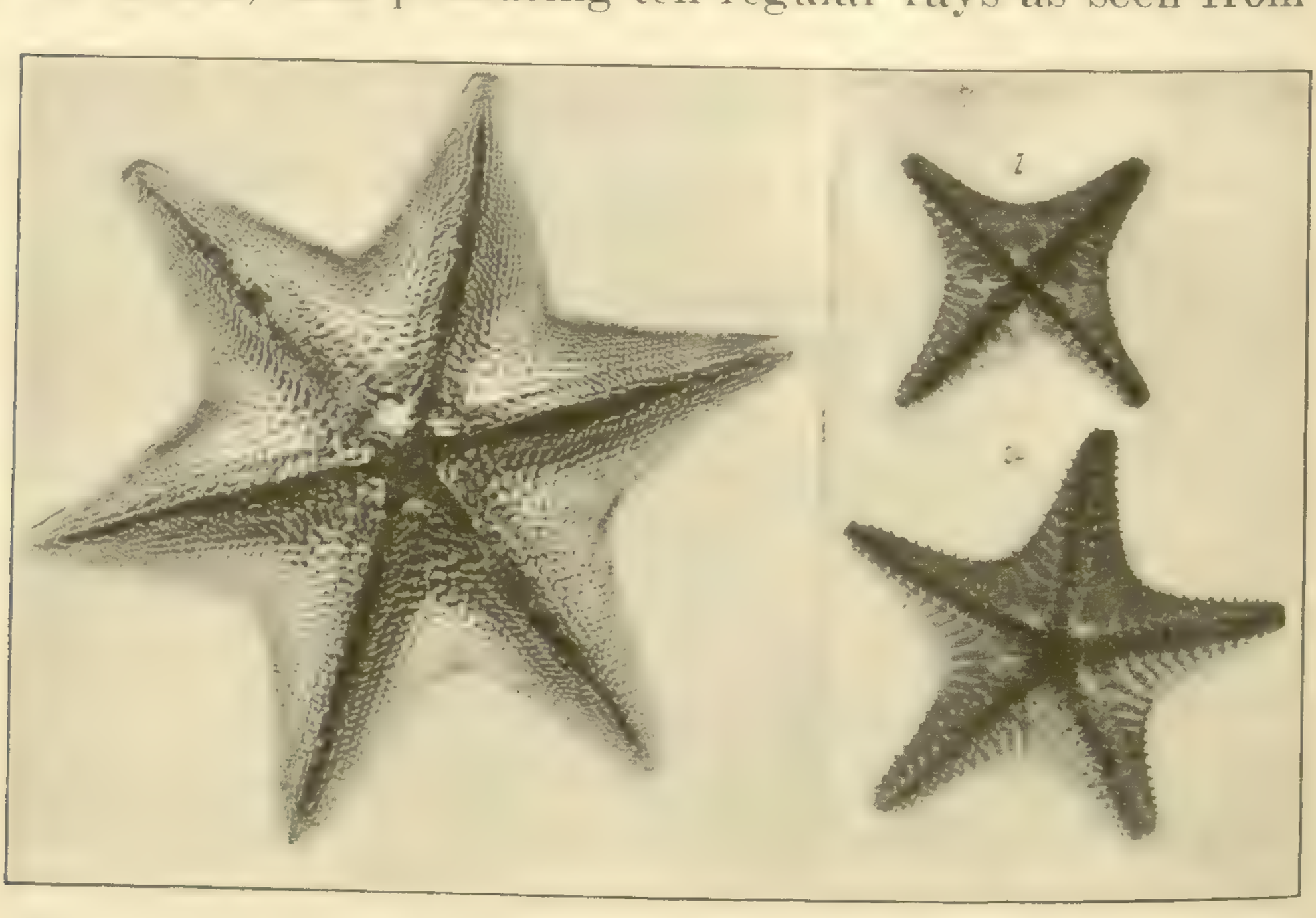


FIG. 2. FIG. 3.

FIG. 2.—*Asterina miniata;* 6-rayed example, reduced.
FIG. 3.—*Ctenodiscus cristatus; a,* normal, underside; *b,* 4-rayed.

above; the forking affects the ambulacral groove and jaw, the corresponding jaw being nearly abortive. The number of rays varies from nine to eleven.

Pisaster ochraceus (Br.). One medium-sized specimen from Monterey and a large one from British Columbia have six regular rays.

Asterias (*Leptasterias*) *hexactis* (St.). Several five-rayed specimens from Sitka agree with the typical six-

rayed ones in size and structural details. One from Vancouver Island has seven regular rays.

Asterias epichlora (Brandt). Although this species was originally described as five-rayed, its normal, or most common condition is six-rayed (var. *alaskensis* Ver., var. nov.), with a more or less evident median dorsal row of small capitate spines, and numerous smaller capitate spines forming a reticulated pattern over the back.[10] One specimen from Victoria has seven rays, due to the forking of one ray about at the middle; another is regularly eight-rayed. The five-rayed form is, perhaps, rather too frequent to be classified under Teratology, but in the several collections of *epichlora* examined by me, at least 90 per cent. of the specimens were six-rayed. The young, carried by six-rayed adults, were all six-rayed.

Ctenodiscus crispatus. Of this abundant species I have from New England a considerable number of regular four-rayed specimens. The few west coast specimens are five-rayed (fig. 3, *a*, *b*).

Significance of Radial Variation; a Problem in Evolution

When we consider the geological antiquity and remarkable persistence of the five-rayed condition[11] in echinoderms, generally, it seems remarkable that so many genera and species of existing starfishes should have acquired the peculiarity of having higher numbers.

All the classes of echinoderms, except perhaps holothurians, had attained highly organized and specialized conditions even in the Ordivician period. With the exception of certain cystidians and a few true crinoids, the

[10] Whiteaves, De Loriol (1897) and others have incorrectly identified *A. Troschelii* as this species. The five-rayed form is apparently the same as *A. saïnichensis* De Loriol, described and figured in 1897, *Mem. Soc. Phys. Geneva*, Vol. XXXII, No. IX, p. 23, pl. ii (xvii), figs. 3–5.

[11] The case is analogous to that of gastropods, which in primordial times acquired the habit of forming right-handed spiral shells, which has prevailed through all the geological ages, though there are some modern families and genera that are normally left-handed, and some species that are as often left-handed as right-handed (Achatinella sp.). No good reason is known why the left-handed condition is not as good as the other.

numerous known Silurian species of crinoids, starfishes, ophiurans and echinoids were regularly five-rayed.

From the Devonian, several genera of starfishes with multiple rays are known. They have the aspect of Crossaster, Labidiaster and Cronaster. But their real affinities are doubtful. Those found in the Mesozoic and Tertiary times, with rare exceptions, are five-rayed.

At the present time all echinoids and holothurians are normally five-rayed. Instances of monstrous specimens with four rays or six rays are very rare in these large and universally distributed groups.[12]

The modern crinoids only rarely depart from the five-rayed condition, even as monstrosities. The ophiurans show more variation in this respect. The common genus Ophiactis, varies, when young, from six-rayed to eight-rayed in nearly all of its species. But such species are usually autotomous, and when adult become regularly either five-rayed or six-rayed.

Ophiocoma pumila, at Bermuda, is about as often regularly six-rayed as five-rayed. *Ophioglypha hexactis* of Kerguelen Island is regularly six-rayed.

I have observed a large, regular, four-rayed example of *Ophiomusium Lymani* from deep water off the New England coast, but it was selected from thousands of five-rayed ones. Other radial variations in ophiurans are known to me, but they are not common, although the species are very numerous and many are often taken in vast numbers.

Among living starfishes radial variations are far more

[12] In the Museum of Yale University there is a full grown, regularly four-rayed example of the sea-urchin, *Arbacia æquituberculata* (Fig. 1, *b*), from the Azores. So far as known to me this is the only known instance in that common species.

Bell (*Jour. Linn. Soc. London*, Vol. XV, p. 126, pl. v, 1880) described a quadriradiate specimen of a sea-urchin, *Amblypneustes formosa*, but it was not quite regularly developed.

Stewart, *op. cit.*, p. 130, described a specimen of *A. griseus* with six ambulacra, but that, also, was somewhat irregularly developed.

Philippi (*Arch. für Naturg.*, 1837, III, p. 241, pl. v) described a quadriradiate *Echinus melo*, which was also a little irregular. A few other cases are known among echinoids.

common than in either of the other classes, as already indicated. But why this is so is a perplexing problem in evolution.

No doubt there are some advantages in the five-rayed condition, or else it would not have remained so constant through all the geologic ages. But it is equally certain that it is more advantageous for certain starfishes, in their special environments, to have six or more rays, otherwise they would not have retained this condition. We must conclude that all these variations originated, at first, as "sports," which have persisted by heredity and natural selection, because they were advantageous. It is easy to conjecture that, in the case of two starfishes, similar in size and structure, living together on a rocky shore and exposed to violent surf, the one with six rays would be able to cling more securely to the rocks than the one with five rays. Therefore, because of the increased number of ambulacral sucker-feet it might well be the form preserved by natural selection, unless for some other important but unknown reason, the five-rayed condition has certain other more important advantages.

It is certainly true that most of the species with multiple rays live among rocks in situations exposed to the surf.[13] This is true of the various shallow water and littoral species of Solaster and Crossaster, which usually have nine to thirteen rays (rarely eight or less). It is also true of the several species of Heliaster with very numerous rays, and many other such species, as well as the numerous five-rayed and six-rayed species of Asterias and Pisaster.

But the power of effectually clinging to rocks may be perfected in other ways, involving an increased number of sucker-feet. This is often attained by lengthening the rays, as in many species of Asterias; by crowding the suckers into more than four rows, as in Pycnopodia and some large species of Pisaster; and by increasing the size and strength of the suckers.

[13] The family Brisingidæ, however, is confined to deep water. All the species are multirayed, with long rays.

These same adaptations would also be useful in enabling the creatures to securely hold their prey, especially while, at the same time, holding fast to the rocks.

I am inclined to believe that the increase of rays has been due more to the advantages gained in holding the food securely than for holding to the rocks, though both go together. The starfishes are the most predacious of the echinoderms. Although they feed largely on gastropods and bivalve mollusks, they also feed on each other, and on large holothurians, echini, and other relatively large creatures.

However, we must admit that, so far as now known, the five-rayed and six-rayed individuals of a species appear to be equally well nourished and grow to equal size. Also that the normally six-rayed species of Asterias are no larger, nor more robust, than the allied five-rayed species, in the same environment. Even the four-rayed individuals, including the four-rayed sea-urchin (Arbacia), mentioned above, appear to be well fed and of average size.

Some, at least, of the many-rayed Brisingidæ use their slender rays for clinging to the deep-sea Gorgonians. I have observed that the *Odinia americana* Ver. thus clings to the branches of *Paragorgia arborea* with its twenty long rays. In such cases numerous rays would be advantageous.

It must be borne in mind that the variation in the number of rays is necessarily attended by extensive changes in the number, size and form of all the skeletal plates; also in the number of ambulacral feet and water tubes, nerve ganglions, nerve cords, stomach lobes, hepatic glands and all other internal organs. A six-rayed specimen has twelve reproductive glands, instead of the ten in its five-rayed competitor. If the number of ovules be proportionately large, it would produce twenty per cent. more young. So, likewise, it would have an additional stomach-lobe and two more hepatic glands. This would, perhaps, be of considerable advantage in the digestion of food and cause more rapid growth. We know that

there is great variation in the size of different individuals of young starfishes of equal age, of the same species, dependent on temperature and relative abundance of food. But I know of no experiments or observations to connect this with the number of congenital rays.

Distribution

A number of Arctic species occur in Bering Sea and as far south as the Aleutian Islands, or somewhat farther. Most of these are circumpolar, as *Crossaster papposus*, *Solaster endeca*, *Henricia sanguinolenta*, *Ctenodiscus crispatus*, *Asterias polaris*, *Asterias hyperborea* (=*A. arctica Murd.*), *A. grænlandica*—*A. cribraria* St. and others.

Some Arctic species are peculiar to the north Pacific side, so far as known, as *Pterasterides aporus* (Ludwig), *Tosia arctica* Ver., *Asterias polythela* Ver., *Allasterias rathbuni* Verrill, *Pteraster octaster* Ver.[14] and others.

But exclusive of the Arctic forms, the entire starfish fauna of the coast, from the Aleutian Islands to San Francisco, is peculiar to that coast, so far as I can determine, and is rather sharply limited, both northward and southward by temperatures only. Some species[15] are closely related to North Atlantic ones, and evidently represent divergent groups derived from a common stock, at no very remote period. However, the cases of greatest interest are those of generic types peculiar to the fauna, some of which have no near allies elsewhere. Among such genera I may mention here a few examples: *Pycnopodia*, with no near allies; *Acantharchaster* Ver., a very isolated genus; *Dermasterias*, with a single species; *Glyphaster* Ver. (type *Leptychaster anomalus* Fisher), with

[14] These last four species are described in the *Amer. Jour. Science*, July, 1909, with others from the same coast.

[15] Among these are *Hippasteria spinosa* Ver., closely related to *H. phrygiana; Leptychaster millespina* Ver., closely related to *L. arctica.* It differs in having smaller dorsal paxilli with fewer spinules, more transversely elongated supero-marginal plates; much finer and more numerous adambulacral spines, four or five in the furrow series. *Mediaster æqualis* St., related to *M. bairdii* V.; *Luidia foliata* Gr., allied to *L. clathrata.* Some of these were evidently derived from Aretic forms.

FIG. 7.

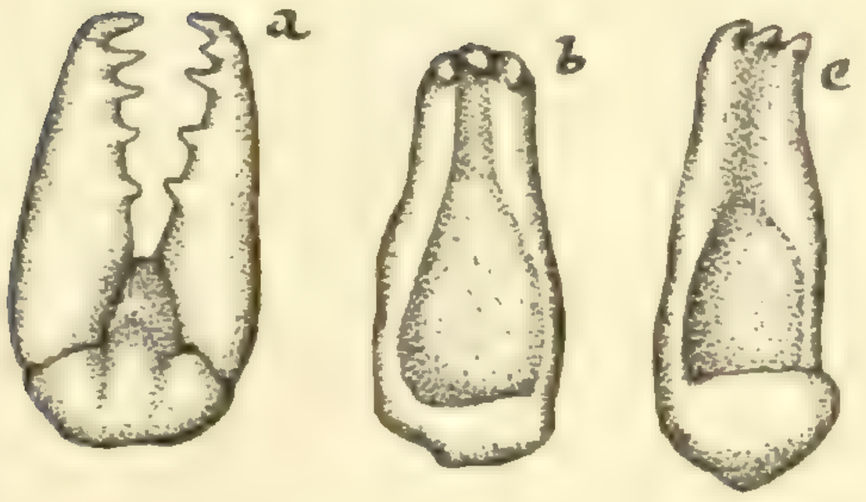
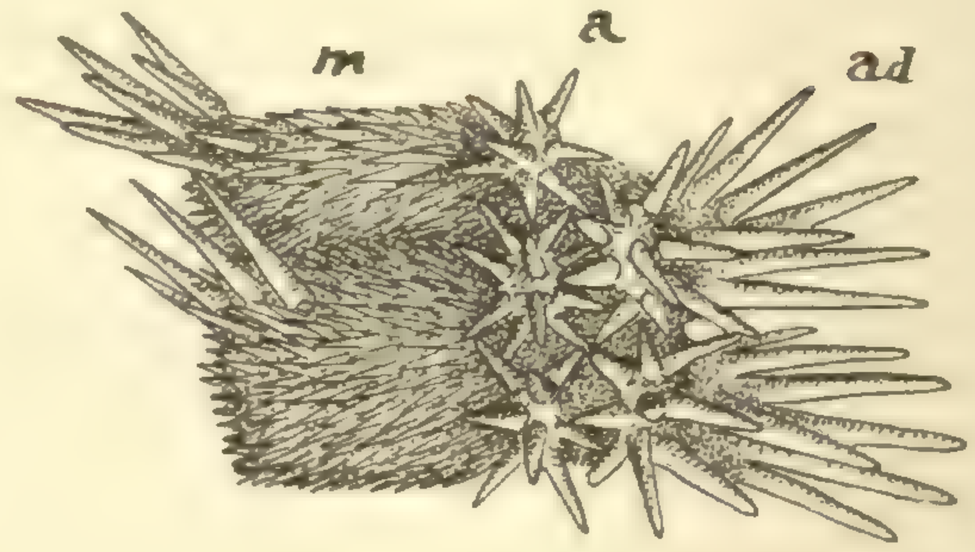


FIG. 4.



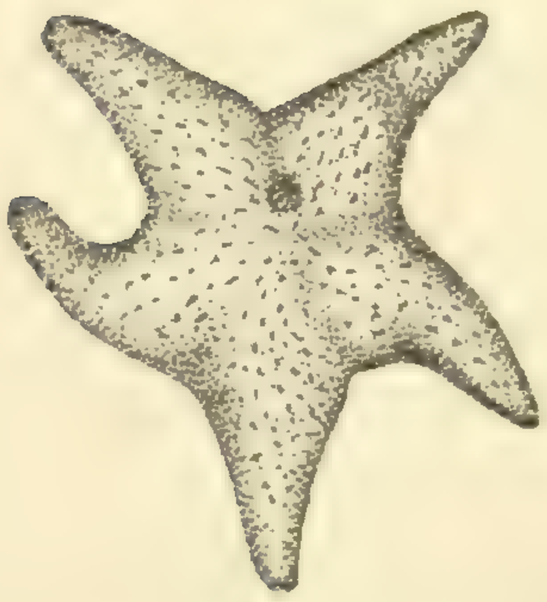


FIG. 5.

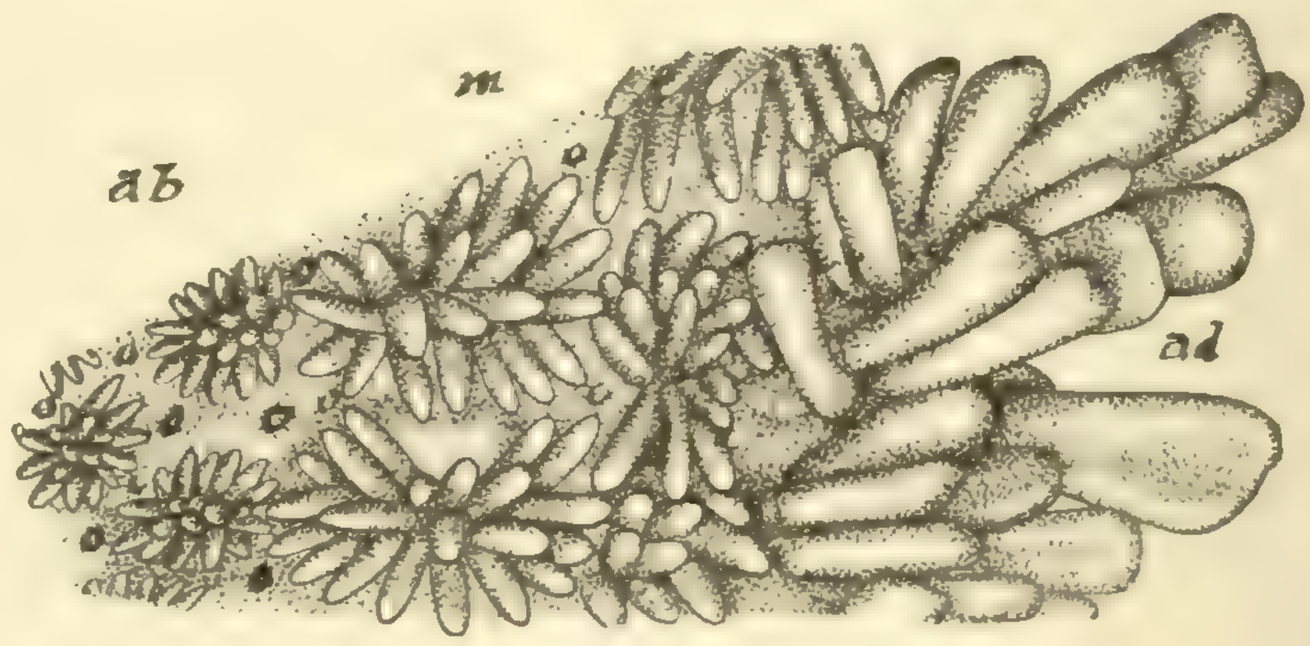


FIG. 6.

FIG. 4.—*Bunodaster Rittori* nov.; *ad*, adambulacral spines; actinals; *m*, marginals.

FIG. 5.—*Henricia tumida* Ver. sp. nov.

FIG. 6.—*H. spatulifera* sp. nov.; *ad*, adambulacral spines; *m*, marginals; *ab*, abactinal pseudopaxillæ; much enlarged.

FIG. 7.—Large unguiculate and denticulate dorsal pedicellariæ of *Pisaster ochraceus*; *b*, *c*, separated valves.

one species (*G. anomalus*): and especially *Pisaster*, which has there eight, large, massive species (mentioned above, p. 542). I am unable to refer with certainty any of the species described as *Asterias*, from other regions, to this group, as restricted, unless it be the six-rayed species, *A. Perrieri* Smith,[16] from Kerguelen I. This agrees with it closely. It is monacanthid and has large dentate pedicellariæ.

Cosmasterias sulcifera (Per.) Sla., from southern South America, is also pretty nearly allied to Pisaster, but is diplacanthid and has few dorsal major pedicellariæ, which are not particularly large. This is the type of Cosmasterias Sla. and it seems better to keep the latter name for this and allied diplacanthid species. It is evident, however, that these Antarctic forms are the nearest relatives of Pisaster.

Bunodaster, gen. nov., resembles Astropecten, but has

[16] *Trans. Phil. Soc.*, Vol. 168, p. 273, pl. xvi, figs. 2–2*b*, 1879.

convex abactinal *pseudopaxillæ;* triangular actinal area of about three V-shaped rows of tesselated plates; curtailed inferomarginals; numerous adambulacral spines. Type *B. Ritteri,* nov. (Fig. 4), has inferomarginals with a distal group of small spines, elsewhere finely spinulose; furrow spines about five to a plate and eight to twelve on actinal side; no spines on superomarginals. California (Prof. W. G. Ritter).

The peculiar northern species, *Allasterias rathbuni,* is represented on the Asiatic coast by *A. versicolor* (Sla. sp. of Japan), which has alternately one and two ambulacral spines, and by *A. amurensis* (Lutk.), Japan to Siberia. Many of the other species of Asteriidæ are only remotely allied to those known in other faunæ. This family and the genus Asterias are world-wide in distribution, but no other region has such a variety of forms.

The family Pterasteridæ is also uncommonly well developed. Seven species have been found in shallow water, besides others in deep water. They all belong to the restricted genus Pteraster, except the remarkable form, *P. aporus* Ludwig, for which I have proposed the new genus Pterasterides (see p. 547, note). It has no dorsal osculum, and the spines around the nephridial or central pore do not reach the marsupial membrane. The Retaster, described by Clark from Puget Sound, I refer to Pteraster (*P. gracilis*). The *P. reticulatus* Ives, which ranges from Puget Sound to middle Alaska, is a very large species and is the most common one. *P. hebes* Ver. and *P. octaster* Ver. are very unlike any species from other regions.

The genus Henricia (formerly Cribrella) is also represented by numerous species and varieties. *H. tumida* Ver., from North Alaska, Cape Fox and C. Disburne, Fig. 1, is remarkable for its large swollen disk and short, stout rays. *H. spatulifera* Ver. southeast Alaska, Fig. 2, is remarkable for its broad paddle-shaped or spatuliform adambulacral spines which are much crowded proximally (see figures).

SHORTER ARTICLES AND CORRESPONDENCE

IS THERE A SELECTIVE ELIMINATION OF OVARIES IN THE FRUITING OF THE LEGUMINOSÆ?

During the past few years I have had occasion to have counted the number of ovules formed per pod in series of many thousands of pods of various species of Leguminosæ. While engaged at this work a side problem of considerable interest presented itself. Since time to follow this up has not been forthcoming for a couple of years, I will publish my data and suggestions for the benefit of any unoccupied botanist.

It is evident that the distribution of ovules, as seen in series of mature pods, does not necessarily represent that of the ovules in the newly formed ovaries. It is possible that the distribution of ovules per ovary in the flower buds may have been modified as the fruits matured by a selective elimination of certain classes of pods. This selective elimination might modify mean or variability or both. One such case is very probably to be found in ovaries with but a single ovule in species normally producing several. If the single ovule be fertilized it may develop into a seed or not, according to various circumstances; but if it fail to develop, the pod will, in most cases at least, fall from the plant. Whether the same factor is at work in the case of ovule classes of a higher order can only be determined by special investigation, but it seems quite possible that such an influence might affect very materially the constants of mature as compared with newly formed ovaries.

In the spring of 1907 I attempted to get some light on this question by the collection of material at different times from individual red bud trees, *Cercis Canadensis*, growing in the North American Tract of the Missouri Botanical Garden.

The flowers of Cercis are produced in an umbel-like cluster from the old wood. These clusters are composed of from two to seventeen flowers. Many of the inflorescences produce only one to four fruits. The per cent. of flowers which mature fruits varies widely from year to year and from tree to tree, but it is evident that there is a very heavy elimination of ovaries. The question to be answered is: Have the eliminated ovaries a dif-

ferent mean or variability, or both, for the number of ovules which they produce than those which develop into mature fruits?

Cercis seems to be a form well adapted to an investigation of this question. The ovaries can be quickly dissected out of the flowers which have been dropped into alcohol for preservation. Absolute alcohol renders the walls sufficiently clear that by the aid of the light from a properly adjusted mirror of the dissecting microscope the ovules may be counted very easily. Clove oil may be used as a clearing agent, but it soon renders the ovules as well as the walls transparent, and great watchfulness is required in the countings.

On March 28 a series of one hundred inflorescences was taken from each of three trees and dropped into alcohol for future study. This was at a time when most of the flowers were open, but when none had fallen from the trees. The whole inflorescence was taken because (*a*) it was desirable to avoid any possibility of an unconscious selection of flowers in gathering, and (*b*) because it seemed desirable to determine whether the position of an ovary on the inflorescence might exert any influence upon the number of ovules produced.

On April 3 a second lot of material was collected, but in an entirely different manner. Many of the blossoms were ready to fall. The trees were shaken, not too violently, so as to secure the flowers which were ready to drop, but not to dislodge those with ovaries which might continue to develop. In preserving this material all the flowers belonging to inflorescences which had fallen were discarded, since it seemed possible that some of them might have been brushed off by twigs rubbing together. All the flowers were open, and, if their very frayed condition may be taken as a criterion, most of them had been visited by insects. The ovaries were dissected out of the flowers at once and dropped into absolute alcohol. Unfortunately the second collection from Tree II was lost.

On April 6 a third collection was made in the same manner as the second.

My intention had been to collect the matured pods of these trees in the fall for comparison with the ovaries taken in earlier stages of development, but, unfortunately, the severe frosts which followed the early opening of spring in St. Louis, in 1907, killed most of the Cercis fruits and precluded the carrying out of this part of the work.

In taking up the counting of the ovules per pod it was found that the alcohol had rendered the material so brittle that it was out of the question to keep the flowers in serial order from the base of the inflorescence, and consequently all attempt at a determination of this point was abandoned for the first collection. As a matter of fact the flowers are so closely grouped in the inflorescence of the red bud that the determination of their sequence would not be easy even in freshly gathered clusters. *A priori*, one would suppose that in an inflorescence so shortened as this, position on the axis would have little influence upon the character of the ovaries. But of course this point should be investigated, for if there is a sensible correlation between position on the inflorescence axis and number of ovules, and between the position of an ovary on the inflorescence and its chances of growing into a mature fruit, this might introduce a serious difficulty into the comparison of eliminated and matured ovaries, in consequence of those of certain types being eliminated merely because of their position on the inflorescence.

TABLE I

FREQUENCY OF NUMBERS OF OVULES PER OVARY IN VARIOUS COLLECTIONS OF CERCIS

Tree.	0	1	2	3	4	5	6	7	8	9	10	?	Totals.
I.—Lot 1					3	1	49	279	476	76	4	11	899
I.—Lot 2				2	1	2	8	113	219	39	3	4	391
I.—Lot 3						1	28	113	179	32	3	2	358
II.—Lot 1	1	1	5	32	177	327	431	100	4			10	1088
II.—Lot 3				2	58	126	112	21	2			1	322
III.—Lot 1			10	23	198	341	179	11				14	776
III.—Lot 2			4	8	85	177	63	5				1	343
III.—Lot 3			2	10	81	170	77	6	1			1	348

The numbers of ovules per ovary for the several series of material are seriated in Table I. In a very small percentage of the cases it was impossible for one reason or another to determine the number of ovules. These cases are placed in the ? column; in calculations they have not been considered, N being reduced by their number. I have no reason to think that these ovaries are in any way different from the others, and so they might have been discarded without comment, but in material of this kind it is best to account for every individual. Perhaps the single entry in the 0 column is due to one of the ovaries being too young.

The constants from Table I are given in Table II.

Regarding first the means, we note that there is no constant difference between those of the different collections. This is true without considering the probable errors, which at once take away any opportunity for theorizing on these points. Inspection shows the same conclusion to be necessary concerning both absolute and relative variabilities.

TABLE II

CONSTANTS FOR OVULES PER OVARY IN VARIOUS COLLECTIONS OF CERCIS

Collections.	Total Ovaries.	Mean and Probable Error.	Standard Deviation and Probable Error.	Coefficient of Variation.
Tree I. Lot 1	888	7.6531±.0172	.7631±.0122	9.9718
Tree I. Lot 2	387	7.7312±.0276	.8070±.0195	10.4386
Tree I. Lot 3	356	7.6235±.0285	.7995±.0202	10.4875
Tree II. Lot 1	1077	5.3556±.0207	1.0091±.0146	18.8429
Tree II. Lot 3	321	5.3052±.0331	.8826±.0234	16.6375
Tree III. Lot 1	762	4.9041±.0216	.8844±.0152	18.0339
Tree III. Lot 2	342	4.8830±.0299	.8224±.0212	16.8426
Tree III. Lot 3	347	4.9567±.0306	.8459±.0236	17.0677

So far as this series of data goes, therefore, we have no reason to think there is any selection in the elimination of the ovaries which do not develop into mature fruits. Most unfortunately the mature fruits are not available for comparison. This renders it necessary to draw the comparisons not between the constants for all the ovaries formed and the fruits maturing, but between the constants for the original population of ovaries and those for the fallen flowers. While not so satisfactory as the former method, the latter is quite justified in the present case, since the second collection represented the first of the ovaries to be eliminated from the tree and the third was taken from the main bulk of those which were to fall. During the last two years I have not succeeded in getting suitable data for the number of the ovules in trustworthy samples of ovaries formed and ovaries maturing in either this or other species of Leguminosæ. In our present dearth of quantitative data concerning selective elimination, this seems a good line to follow far enough to get conclusive positive or negative results. Perhaps some other botanist can collect adequate masses of data.

J. ARTHUR HARRIS.

CARNEGIE INSTITUTION OF WASHINGTON,
COLD SPRING HARBOR, L. I.

NOTES AND LITERATURE

ICHTHYOLOGY

Ichthyological Notes.—The State Laboratory of Natural History of Illinois has published an elaborate work entitled "The Fishes of Illinois," by Dr. Stephen A. Forbes and Robert Earl Richardson. In this work is given a full account of the topography of the state of Illinois, with excellent descriptions of all the species of fishes found in the state. Many of these are illustrated by colored plates, and the work is done with admirable conscientiousness and accuracy. An especial feature of the work is the very full account of the food of the different species of fishes.

In the *Proceedings of the United States National Museum* (Vol. XXXV, 1908), Professor J. O. Snyder describes eighteen new species of fishes from southern Japan and from the Riu Kiu Islands. Professor Snyder was the first ichthyologist to visit this most interesting group of islands.

In the same *Proceedings,* Professor Theodore Gill shows that the name Chœrodon is the oldest name for the genus commonly called Chœrops.

In the same *Proceedings,* Professor Snyder describes two rare fishes, from California, *Rimicola eigenmanni,* with which *R. muscarum* is identical, and *Plagiogrammus hopkinsi.*

In the *Proceedings of the Academy of Natural Sciences of Philadelphia* (1908), Henry W. Fowler gives an excellent synopsis of the Cyprinidæ of Pennsylvania, with notes on the material examined by Professor Cope. One new species, *Notropis keimi,* is described from the Allegheny River.

In "Annales de la Société Géologique du Nord" (T. XXXVI, 1907), Maurice Lariche presents observations on the fossil fishes of Patagonia, showing that the species of shark recently described as Cretaceous belong to the lower Miocene.

In the same *Proceedings* (T. XXXV, 1906), Lariche gives a review of the fossil fishes of the north of France. In his nomenclature he pays little attention to the law of priority.

In the same *Proceedings,* Lariche records various fossils from Brittany and other parts of France.

In the *Bulletin of the Geological Society of Belgium* (1908), Lariche records the presence of a species of Amia in the Hampstead Beds of the Isle of Wight.

In "Comptes rendus de l'Association Française pour l'Avancement des Sciences," Congress of Lyons (1906), Lariche describes and figures numerous species from Tertiary rocks near Montpellier.

The same author describes, in the "Annales de l'Université de Lyon" (1908), the vertebrates of the Nummulitique de l'Aude.

In the *Bulletin of the Museum of Natural History*, of Paris (1908), Dr. Jacques Pellegrin describes numerous characins from South America.

In "La Revue Coloniale" of Paris (1908), Dr. Pellegrin discusses the fresh water fishes of French Guiana, with their vernacular names.

In the *Bulletin of the Southern California Academy of Sciences* (1909), Mr. J. Z. Gilbert publishes an account of certain California flounders, with a figure of an unnamed fossil flounder from Miocene rocks at Lompoc, California. This species belongs to the large-mouthed group, with very strong teeth, but the body cavity is considerably larger than in the related species of the present time. The species will soon be described in detail by Mr. Gilbert.

In the *Proceedings of the Academy of Natural Sciences of Philadelphia* (1908), Professor Snyder describes the large ribbon-fish from Monterey Bay, California, under the name of *Trachypterus seleniris.*

In the *Proceedings of the New York State Teachers Association* for 1907, Dr. Wilder discusses the usefulness of the dog-fish for educational purposes.

In the *Proceedings of the American Philosophical Society* for 1908, Dr. Wilder discusses the brain of the extraordinary Japanese Chimæra, *Rhinochimæra pacifica.* Dr. Wilder looks forward to the time when "no child shall reach the age of ten without exposing for himself, drawing, describing and dissecting the brain of some shark."

In the *Popular Science Monthly* (October, 1908), Professor W. S. Tower describes "The Passing of the Sturgeon" in America, the five species being practically exterminated all at once by murderous fishing methods. The most aggravated case

of this kind is the destruction of the species inhabiting the Lake of the Woods by Michigan fishermen who took them by thousands from their spawning beds in Rainy River, preserving the eggs for caviar and throwing the bodies away.

In the *Biological Bulletin*, XIV (1908), B. G. Smith records the spawning habits of the minnow Chrosomus, this work being part of a series of investigations undertaken by the advanced students of Professor Jacob Reighard, of the University of Michigan.

In the *Bulletin of the Bureau of Fisheries* (Vol. XXVII, 1907), Professor Snyder records the "Fishes of the Coastal Streams of California," *Hybopsis crameri*, *Rhinichthys cormanni* and *Ptychocheilus umpquæ* are described as new species from the Umpqua region in Oregon, and *Catostomus humboldtianus* from Humboldt County, California. Professor Snyder shows that *Leuciscus caurinus* is a species of Leuciscus, and not identical with *Mylocheilus lateralis*. Professor Snyder gives an interesting map of the coastwise streams, showing the distribution of the different faunal groups.

In the same *Bulletin*, Professor Snyder discusses the "Fish Fauna of the Lakes of Southeastern Oregon" with reference to the distribution of the different forms. *Catostomus warnerensis* and *Rutilus oregonensis* from Warner Lake, and *Rutilus columbianus* from the Columbia River, are described as new species. A map of the isolated Warner Lake region, the remains of Lake Idaho, is given.

In the same *Bulletin*, the paper on the habits and distribution of fishes in the Sacramento Basin, by the late Cloudsley Rutter, is published. The manuscript, prepared before the death of the lamented author, who was one of the most careful observers of fishes connected with the Bureau of Fisheries, has been revised by Dr. Evermann. In this paper, *Catostomus microps*, *Cottus asperrima(us)* and *Cottus macrops*, new species from Modoc County, California, are described.

In the same *Bulletin* (1908), Jordan and Richardson describe the fishes collected in the Philippines by Richard Crittenden McGregor. Eleven new species are described and figured, and two hundred and ninety-five species are mentioned with critical notes.

In the *Hamburger Magalhænsische Sammelreise* (1907), Pro-

fessor Einar Lönnberg describes the species taken in the Straits of Magellan.

In the Publications of the Department of Education of Ontario (1908), Mr. C. W. Nash, of Toronto, publishes a catalogue of the fishes of Ontario, with plates of many of the more important species. This is prepared primarily for the use of the teachers of Ontario, and is part of a volume containing all the vertebrate animals. It will prove extremely useful for the purposes for which it was prepared.

In a report of the Biological Survey of State of Michigan (1907), Thomas L. Hankinson gives a biological survey of Walnut Lake, with numerous plates, photographs and other illustrations, showing the nature of the fauna and flora.

In the Michigan Academy of Science, Mr. Hankinson gives a list of fishes of Hillsdale County, Michigan.

In the *Annuaire du Musée Zoologique de l'Académie Impériale des Science de St. Pétersbourg* (T. XIII, 1908), L. Berg gives a list of the fishes of the River Kolyma, with descriptions, mostly in Russian, of the various species found there.

In the same *Annuaire* is given a list of the fishes of the River Obi.

In the *Journal of the College of Sciences of the Imperial University of Tokyo* (1908), Shigeho Tanaka describes six new species and two new genera of fishes from Japan, with notes on other rare forms.

In the *Annotations Zoologicæ Japonenses* (1908), Tanaka gives a description of eight additional new species from Japan.

In the same *Journal* (1908), Tanaka describes "Tide-Pool Fishes of Misaki, Japan," with two additional new species.

In the same *Journal*, Tanaka records the fishes of Lake Biwa, with one new species.

In the *Zoological Magazine* (1908), Tanaka again records, in Japanese, the fishes of Lake Biwa, the largest of the Japanese lakes.

In the *Transactions of the Natural History Society of Sapporo*, Professor K. Otaki describes the Stickle-backs of Japan, in Japanese and in English, one new species being described.

In the same *Transactions*, Professor Otaki describes the common sturgeon of northern Japan, *Acipenser mikadoi*.

In the *Sitzungsberichten of the Vienna Academy* (1908), Dr.

Viktor Pietschmann describes the sharks of Japan, with descriptions of some new species.

In the same *Sitzungsberichten*, Dr. Pietschmann describes also two new Japanese species of shark, and he has also a paper comparing the European species of *Mustelus* with each other.

In the Smithsonian Miscellaneous Collections (1908), Professor Gill gives in detail the story of the devilfish, Manta, with numerous illustrative plates.

In the *Proceedings of the Zoological Society of London* (1908), Dr. Regan gives a valuable revision of the sharks of the family Orectolobidæ. To this family he refers Rhinodon, Gingly-mostoma and other forms usually placed in separate families.

In the *Annals and Magazine of Natural History* (1908), Mr. Regan describes a collection of fresh-water fishes from Costa Rica, with several new species. *Joturus stipes*, from Central America, is made the type of a new genus, Xenorhynchichthys. A new genus, Tomocichla, near Herichthys, is also described.

In the same *Annals*, Mr. Regan discusses the systematic position of Stylophorus, which he places near the Allotriognathi. He discusses the work of Professor Starks on the same species, who, in the *Bulletin of the Museum of Comparative Zoology*, for 1908, makes Stylophorus the type of a new suborder, Atelaxia. The work of both of these anatomists shows that Stylophorus is related to Trachypterus and also to Velifer.

In the same *Annals*, Mr. Regan revises the species and subspecies of Coregonus found in Great Britain.

In the same *Annals*, Mr. Regan revises the char of Great Britain, adding a number of new species. Four old species and five new ones are recognized in place of the single *Salvelinus alpinus*, recognized by Day as found in British waters.

In the same *Annals*, Mr. Regan describes the species of char, six in number, found in the rivers of Ireland. He recognizes the fact that these species are of relatively recent date, and perhaps only partially separated from one another.

In the same *Annals*, Mr. Regan discusses a classification of the scombroid fishes, or mackerel-like fishes. He recognizes the extremely close relation of the Carangidæ with the perch-like forms, or Serranidæ.

In the same *Annals*, Mr. Regan revises the genus Elops, showing that instead of a single species, *Elops saurus*, there are seven well-marked species. This conclusion the writer has been

able to verify in part, having specimens of *Elops hawaiensis* from Formosa as well as from Hawaii. Regan describes *Elops affinis*, from Mazatlan and Jalisco, the species being based on a specimen sent as *Elops saurus* by the present writer.

In the same *Annals* (1909), Mr. Regan takes up the impossible problem of defining the orders and sub-orders and equivalent groups of the teleostean or bony fishes. The paper is most suggestive and valuable, but no one adjustment of the intricate interrelationships of these fishes is likely to be more permanent than any other. It is encouraging, however, to notice the practical agreement between Mr. Regan's classifications and those adopted by American naturalists in matters in which the facts have become clearly apprehended.

In the same *Annals*, Mr. Regan gives an account of the fishes of the group Salanginæ, mostly of eastern Asia.

In the same *Annals*, Mr. Regan gives an account of new fishes from Lake Candidius, in Formosa.

In the *Annals of the South African Museum* (1908), J. D. F. Gilchrist and W. W. Thompson give descriptions of fishes from the coast of Natal, with descriptions of numerous species.

In the same *Annals*, Gilchrist and Thompson give an account of the blennies of South Africa, the species referred to Clinus being especially numerous.

In the *Annals of the Queensland Museum*, J. D. Ogilby describes numerous new or little-known fishes from the Queensland Museum in Brisbane. Among other things, he claims that the name Dampieria should supersede Labracinus, recently resurrected to take the place of Cichlops, which is preoccupied.

In the Publications of the Department of Fisheries for New South Wales, David G. Stead gives an interesting account of the beaked salmon, Gonorhynchus.

In the same Publications Mr. Stead gives descriptions of three new species of fishes from New South Wales.

In the *Proceedings of the Royal Society of Queensland* (1907), Mr. J. D. Ogilby describes seven new species of fishes from the coast of Queensland. He divides the genus Tylosurus into three, separating from it Stenocaulus, with body short and deep, the type being *krefftii*, and Eurycaulus, with the caudal peduncle strongly keeled, the type *platyura*.

In the same *Proceedings*, Mr. Ogilby describes numerous new species and genera of fishes from Queensland.

In the "Scientific Investigations of the Fishes of Ireland" (No. V, 1908), Holt and Byrne record certain fishes of the Irish Atlantic Slope.

In the *Bulletin of the Department of Agriculture in the Dutch East Indies* (1908), Van Kampen describes the larva of Megalops, which passes through changes similar to those already recorded for Albula.

In the Norwegian journal *Naturen* for 1908, Stejneger discusses in Norwegian the species of char found in Norway, *Salvelinus salvelinus* and *Salvelinus alpinus*.

In the *Journal of Comparative Neurology and Psychology* (Vol. XVIII, No. 6, 1908), Professor J. B. Johnston describes in detail the nervous system of the lamprey.

In the same *Journal*, Professor Johnston further discusses the physiology of the nerves of the lamprey.

In the *Anatomical Record* (Vol. II, No. 6, 1908), Professor Johnston discusses the question of the presence of the glossopharyngeal nerve in the hagfish.

In the same *Journal*, Professor Stockard gives a note on the same subject.

In the *Zoologischen Jahrbuchern of Jiessen* (1908), E. P. Allis, Jr., discusses the bloodvessels in various bony fishes.

In the same *Journal*, Dr. E. Philippi discusses the name and development of certain viviparous fishes of the genus Glaridichthys.

In the American Breeders Association (Vol. IV), the Committee on Breeding Fish, J. W. Titcomb, Chairman, discuss the possibility of improvement of fish stock by selective breeding.

In the *Memoirs of the Royal Society of Copenhagen* (1908), Dr. H. F. E. Jungersen gives an elaborate account of the genera of fishes related to Centriscus. This is a most valuable contribution to our knowledge of the fishes of this type, and ought to help settle the questions as to their relationship to other related forms.

In the *Transactions of the Royal Society of Edinburgh* (Vol. 45, 1907), W. E. Agar gives a valuable account of the paired fins in Lepidosiren and Protopterus, with special reference to the nerve structures.

In the Annual Report of the Department of Marine and Fisheries for Canada, are given valuable studies of the effect of dynamite explosions and sawdust on fish life. The evil effects

of dynamite are here clearly emphasized by Professor A. P. Knight. Professor Knight does not, however, find the effect of sawdust as injurious as has been hitherto supposed. A strong solution of sawdust poisons fish and fish fry, through the agency of compounds dissolved out of the wood cells. Fishes will desert a river polluted with freshly made sawdust, going down stream or into tributaries to escape from the disagreeable influence of the sawdust extracts. Waste matters which would be deadly in one river will pass away and prove of little harm in another, where the conditions are different.

In the *Journal of Morphology* (1908), Reighard and Mast describe the development of the hypophysis of Amia.

In the *Journal of Experimental Zoology* (1909), Professor C. R. Stockard describes the development of the young of *Fundulus heteroclitus* in magnesian solutions instead of salt water. The result is the development of cyclopean fish, with a single coalesced eye on the top of the head. It is thought that magnesia possesses an anesthetic effect, and is inhibitory in its influence on muscular activity. It, therefore, retards the out-pushing of the eyes in the embryo, leaving the eyes without energy for perfect development, and at times without energy sufficient for their normal separation.

In the *Outing Magazine* (September, 1908), Bonnycastle Dale describes the mystery of the salmon, and its desperate struggle to breed in the waters of the Columbia, with some excellent photographs.

Under the head of "The Fishes of Japan," Otaki, Fujita and Higurashi continue their fifth volume of discussion of the Japanese fisheries and fishing methods. The fourth volume contains colored plates of a number of Japanese food fishes. The text is entirely in Japanese.

DAVID STARR JORDAN.

PARASITOLOGY

The question as to the relation of the tse-tse fly which is absolutely demonstrated to be the transmitting agent of sleeping sickness and the parasite of the disease is one that has been discussed pro and con with great vigor. Minchin and others contend most powerfully that the fly is a mere mechanical vector while Manson and his supporters, chiefly, it must be confessed,

from a theoretical standpoint, have maintained that the fly stood in the same relation to the disease as the mosquito held to malaria. As already indicated, the definite evidence thus far secured has seemed to favor the view that the fly is a mere mechanical agent. Some recent experiments in East Africa are of tremendous importance in this discussion. Kleine[1] under date of December 28, 1908, reports from Kirugu, German East Africa, an experiment which apparently demonstrates that flies may infect after a long interval. Heretofore it has been claimed that flies would not infect later than forty-eight hours after biting infected hosts. A longer interval is good evidence of the existence of a developmental cycle in the fly. Kleine's experiment may be summarized as follows:

Nagana, an animal disease due to *Trypanosoma Brucei*, does not occur in the Kirugu region. Animals which had been naturally infected by the bite of the tse-tse fly, *Glossina morsitans*, were brought from a locality seven days' march distant and were kept in isolation. Other flies, *Glossina palpalis*, caught on the Mori River, were fed for three days on the infected animals and from the fourth to the seventeenth day inclusive for each day on a fresh healthy animal. From the eighteenth to the twenty-fourth day the flies fed on a single sheep; from the twenty-fifth to the twenty-ninth day on a single ox. Frequent blood examinations were made of the experimental animals and on the twelfth day after the flies were put on the ox which was first used on the twenty-fifth day of the experiment, numerous trypanosomes were found in the blood of this host. Then the sheep first employed as host on the eighteenth day was examined and found also to be infected. All the other experimental animals remained uninfected. Goats, calves and sheep were used to feed the flies from the fortieth to the fiftieth day and all were infected. The author concludes: "From this it is seen that flies which for many days after the ingestion of blood containing trypanosomes were not infective, afterwards became so and infected a sheep and then an ox."

The Royal Society has received a telegram dated April 3 from Colonel Sir David Bruce which announces the confirmation of Kleine's observations, and a letter received April 30, dated Mpumu, Chagwe, Uganda, April 3, confirms the cablegram

[1] "Positive Infektionsversuche mit *Trypanosoma Brucei* durch *Glossina palpalis*." *Deutsche medizinische Wochenschrift*, 18 Marz, 1909; 469–470.

notice and says that the Commission had "repeated Dr. Kleine's experiments with *Trypanosoma gambiense* and *Glossina palpalis*, also with a trypanosome of the *dimorphon* type and the same tse-tse flies and found the flies infective after 16, 19 and 22 days."

It is apparently impossible to escape the conclusion that the parasite of human sleeping sickness, *Trypanosoma gambiense*, also undergoes a cycle of development in its transmitting agent, *Glossina palpalis*, and that the fly bears the same relation to the parasite which the mosquito does to the malarial organism. It is unnecessary to indicate in detail the tremendous importance of this discovery.

Old fables die hard and among them must be placed the oft-repeated story cited in many modern texts of good standing that in some parts of Italy and France the population makes use of certain fish tapeworms (Ligula) which are found in the body cavity of various cyprinids, as a delicacy under the name of macaroni piatti or ver blanc. In 1894 Monticelli demonstrated the incorrectness of the story, but it continues to be cited as a biological marvel even by recent writers of repute. Recently Parona has again exploded the myth in an interesting brochure entitled "Les Liguliphages ou soi-distant mangeurs des ligules."[1] Nowhere in Italy is such a habit found; the error is as persistent as false and deserves general contradiction until it is finally eliminated from our text-books. Rudolphi reported that at times the Ligulæ are eaten with the tench which they infest, being taken for the fat of the fish. From such a simple beginning the fable grew until it was said that certain fish culturists raised tench to obtain the ligulæ which they harbored. The final stamp of reality was imparted to the fable when a French savant wrote that these biological noodles are eaten at Lyons as in Italy!! Like the tales of early naturalists, which Linné copied so faithfully, that tapeworms occur in brooks and springs, so let the marvellous story of the liguliphages be consigned to the care of writers on unnatural history and forever more be eliminated from serious consideration.

Sambon and Seligman[2] have recorded studies on the haemogregarine of reptiles, describing many new species and affirming

[1] *Bull. pop. pisiculture*, n. s., 4.
[2] *Jour. Trop. Med.*, December, 1908.

that their life history manifests two cycles; the schizogonic or vegetative cycle, in the blood of vertebrates and characterized by asexual multiplication with the sporogonic, characterized by sexual reproduction. They enumerate merozoites, schizonts, sporonts, etc. Patton[3] recounting his work on the same objects states that careful feeding operations with larval nymphal and adult ticks under most favorable conditions at the King Institute, Madras, and several years' study of similar parasites in amphibia and their transmitting leeches, for comparative purposes, have entirely failed to elucidate the extra-corporeal life histories of the intracellular parasites of either reptiles or mammals. He regards the transmission of these parasites as mechanical and questions the interpretation of the different forms described by the other authors from the peripheral blood of snakes. He inclines to consider all their forms as belonging to a single species of hæmogregarine and in closing calls attention to Prowazek's error in regarding cysts found in a pentastome from a python as developmental stages of *Hæmogregarina pythonis* when in reality they represent part of a cycle of a parasite peculiar to the pentastome and have nothing to do with the hæmogregarine of the snake. Patton might have cited numerous similar cases of confusion between normal parasites of a supposed transmitting agent and the missing developmental stages of the parasite under investigation.

In the same journal[4] Patton gives a brief though valuable résumé of the genus *Herpetomonas* which emphasizes certain points of great importance in this connection. These flagellates are parasitic in the alimentary tract of insects, though those which occur in blood-sucking insects are in no wise related to blood parasites. Their developmental cycle consists of a preflagellate, a flagellate and a postflagellate stage. The preflagellate stage presents round or oval bodies with nucleus and blepharoplast, multiplies by simple longifission or multiple segmentation, and occurs in the insect's mid gut. In the flagellate stage the organism forms a single flagellum and is found in both mid gut and hind gut, while the postflagellate stage is characterized by massing of the herpetomonads in the midgut and the formation of cysts which pass out in the feces. Many are undistinguishable in their preflagellate stages and a partial study

[3] *Parasitology,* December, 1908.
[4] *Parasitology,* December, 1908.

may lead to confusion of true herpetomonads with Crithidia or young trypanosomes, such as has actually occurred in more than one instance.

He closes thus:

As the life-cycles and general structure of the three human parasites are similar to those of well-known Herpetomonads, I see no reason for placing them in a distinct genus. The differences in their development, such as the formation of the flagellum, methods of division and the fact that their preflagellate stages are passed in man only justify their being regarded as specifically distinct from such species as *H. muscæ-domesticæ*, *H. sarcophagæ*, *H. culicis*, *H. lygæi* and many others.

In the opinion of others, just the points noted justify including the three human parasites in a separate genus, Leishmania.

H. B. Ward.

PLANT CYTOLOGY

The Permanence of Chromosomes in Plant Cells.—The problem of the individuality of the chromosome is receiving the attention of a number of plant cytologists. Briefly stated the problem concerns the permanence of the chromosome as an organ of the cell, enquiring whether the chromosomes are present as structural entities in the resting nucleus and whether they have come down from a line of ancestral structures reproducing by fission in the mitoses throughout the life histories.

In 1904 Rosenberg presented claims that the chromosomes may be recognized in the resting nuclei of certain plants and cited *Capsella bursa-pastoris* as a favorable type for their demonstration. Overton in 1905 traced the chromosomes of certain dicotyledons to aggregates of chromatin in the resting nuclei which he designated as prochromosomes, believing them to be autonymous structures representing the chromosomes in this stage of nuclear activity. Other investigators have reached similar conclusions. Nevertheless a number of plants is known in which the forms of the chromosomes during the interkineses are so changed by progressive alveolization or vacuolization as well as by the reticular union of chromatic masses through anastomoses that the outlines of the structures can not be followed in the irregularities of the chromatic and linin network. Whether the chromosomes in such nuclei really lose their identity as autonymous structures is not of course established simply by the negative evidence that they have not been traced

by the technical methods at our command. These difficulties, however, have been clearly set forth by Mottier and other authors, some of whom are unwilling to accept the hypothesis of the permanence of the chromosome.

Four papers have recently appeared which give further evidence of the presence of prochromosomes in the resting nucleus and also present some important conclusions on the history of the chromatin during synapsis. In the latter feature these authors (Overton, Lundegardh and Rosenberg) support the view that during synapsis the sporophytic chromosomes by the parallel association of two spirems become grouped in pairs to form the reduced number of bivalent chromosomes characteristic of the heterotypic mitosis.

Overton[1] presents the results of studies on the pollen mother-cells of *Thalictrum purpurascens*, *Calycanthus floridus* and *Richardia africana*. He finds that the sporophytic (somatic) nuclei previous to the heterotypic mitosis have their chromatin in the form of definite bodies arranged in pairs with linin intervals between. The bodies are prochromosomes and were traced through synapsis to the chromosomes of the heterotypic mitosis. Overton interprets the grouping of the prochromosomes in pairs to mean that there are two spirems of paternal and maternal origin in the sporophytic nuclei which he believes remain distinct throughout the sporophytic phase of the life history. The parallel threads become more distinct just before synapsis and become very closely associated during the synaptic contraction, but remain distinct from one another.

The association of the sporophytic chromosomes in pairs is most intimate during postsynaptic stages when these elements become more or less closely united in various ways to form the bivalent chromosomes (in the reduced number) characteristic of the heterotypic mitosis. This is the period in the life history when the sporophytic chromosomes are most likely to influence one another by conjugation or by the mutual interchange of substance.

The first or heterotypic mitosis in the pollen mother-cells distributes the sporophytic chromosomes associated in pairs. At this time each sporophytic chromosome undergoes a longitudinal

[1] Overton, J. B., "On the Organization of the Nuclei in the Pollen Mother-cells of Certain Plants, with Especial Reference to the Permanence of the Chromosomes," *Ann. of Bot.*, XXIII, p. 19, 1909.

fission in preparation for the second or homotypic division so that chromosome tetrads are present during the metaphase of the heterotypic mitosis. The split chromosomes remain distinct during the interkinesis between the two mitoses and the halves are distributed by the homotypic division to the nuclei of the pollen grains.

The nuclei of the pollen grains show prochromosomes arranged in a single series and it seems probable that they retain this arrangement throughout the gametophytic phase of the life history. It also seems probable that the fertilization of the egg nucleus effects the close association of two such series of chromosomes, thus accounting for the pairs of prochromosomes arranged on parallel threads, and that this association is maintained throughout the history of the sporophyte until the distribution of the sporophytic chromosomes by the heterotypic mitosis. Nevertheless it is but fair to point out that these inferences are not as yet supported by direct evidence, that is to say, the history of the chromosomes has not been followed throughout the life history of any of these seed plant.

Lundegardh[2] introduces his paper with a good summary of the two views concerning the origin of the bivalent chromosomes of the heterotypic mitosis, (1) the theory of the parallel association of two spirems (Junktionstheorie), and (2) the theory of the folding of a single spirem (Faltungstheorie). His investigations are based on several types of the *Compositæ* (*Calendula officinalis, Achillea millifolium, Anthemis tinctoria* and *Matricaria chamomilla*), and on *Trollius europæus* of the *Ranunculaceæ*. Unfortunately these forms are not treated serially but with reference to the critical phases of the processes of the reduction divisions so that it is very difficult for the reader to follow the text and figures consecutively for any of the types. The difficulty is further increased by the crowding and ill arrangement of the figures. In deference to the reader too much care can not be given to these matters.

Lundegardh finds for the types of the Compositæ that the prochromosomes (*Gamosomen*) are generally arranged in pairs (*Gamomiten*) in the resting nucleus of the pollen mother-cell. In Trollius, on the other hand, the chromatin is in the form of numerous granules distributed on a delicate linin network and

[2] Lundegardh, H., "Ueber Reduktionsteilung in den Pollenmutterzellen einiger dicotylen Pflanzen." *Svensk. Bot. Tidsk.* III, p. 78. 1909.

prochromosomes could not be recognized. As the nuclei of these Compositæ approach synapsis the pairs of prochromosomes become connected with one another by delicate threads along which the chromatic substance is distributed so that two parallel systems of threads are constructed which finally become so closely associated as to form a single spirem. The chromatin granules of Trollius gather and fuse into larger masses which are at first more numerous than the chromosome count but show a tendency to pair. These are distributed over a delicate linin network upon which the chromatin becomes distributed. Finally the chromatic masses fuse thus forming a single spirem.

The later history of the reduction processes is similar in all of the types. The spirem splits (strepsinema stage) and segments into the reduced number of bivalent chromosomes which become distributed in the nuclear cavity (diakinesis) as pairs of chromosomes. The halves of the split segments of the spirem may then be regarded as the sporophytic chromosomes to be distributed in two sets by the heterotypic mitosis. A contraction during the strepsinema stage (second contraction) is not regarded as of special significance, but merely as an accompaniment of this period in the development of the bivalent chromosomes. The phenomenon of synapsis is regarded as especially significant since it is the period when the sporophytic chromosomes are in their most intimate relation to one another.

Rosenberg in two recent papers gives additional evidence in support of his belief (1904) in the permanence of the chromosomes, and develops further his views on the significance of synaptic phenomena. The first paper[3] deals especially with *Hieracium venosum* and *H. auricula*. A brief introduction outlines clearly the problems concerned with the prochromosome or gamosome theory and their relation to the views on the interpretations of the events of synapsis and the reduction divisions.

The chromatin is present in the resting nuclei of the archesporium as irregular deeply-staining masses almost always situated at one side of the nucleus. These are interpreted to be prochromosomes or gamosomes, their number corresponding generally to the number of chromosomes which for the sporophyte is fourteen and eighteen in these two species of Hieracium. As the nuclei of the pollen mother-cells approach synapsis the prochro-

[3] Rosenberg, O., "Zur Kentniss der präsynaptischen Entwicklungsphasen der Reduktionsteilung," *Svensk Bot. Tidsk.*, I, p. 398, 1907.

mosomes are found associated in pairs distributed over a network. The further history of the reduction mitoses is not described, so that the investigation is incomplete in a number of important features.

The second paper of Rosenberg[4] deals with *Crepis virens*, one of the Compositæ, a form remarkable for the small number of chromosomes, which are six for the sporophyte and three for the gametophyte generation. A further important peculiarity is a difference in the size of the chromosomes which makes it possible to follow the individual elements through succeeding mitoses with some degree of certainty. This is, so far as the reviewer is aware, the first account for plants of such a differentiation of chromosomes as has been described for animals by a number of zoologists.

The nuclei of the sporophyte (somatic) show six small prochromosomes in the resting stage from which are organized during the prophases of the vegetative mitoses two short rod-shaped chromosomes, two very long bent elements, and two chromosomes about midway in length between these extremes. The resting nuclei of the pollen mother-cells have six prochromosomes more or less clearly grouped in pairs. Synapsis presents a series of parallel threads intimately united at intervals. From this condition a thick coiled spirem is organized which clearly shows its double nature in the frequent longitudinal separation of portions as though it were split. The free ends of the chromosomes composing the spirem may at times be distinguished. A gradual contraction of the spirem leads through stages comparable to those described as a second contraction by various authors to the period when the six chromosomes, grouped in three pairs, may be clearly recognized (diakinesis).

The chromosome group on the approach of the heterotypic mitosis consists then of a pair of small, almost spherical, chromosomes, a pair of long rods, and a pair of short rods. These correspond to the three different sizes of chromosomes present in the vegetative sporophytic mitoses, but are more condensed or shortened. Thus the heterotypic mitosis is a true reduction division distributing the six chromosomes in two sets each of which consists of a spherical chromosome, a long rod, and a chromosome intermediate in shape between these two. These

[4] Rosenberg, O., "Zur Kenntniss von den Tetradenteilungen der Compositen," *Svensk Bot. Tidsk.*, III, p. 64, 1909.

chromosomes divide during the anaphase of the heterotypic mitosis in preparation for the second or homotypic mitosis so that they appear at the poles of the heterotypic spindle in the form of three split chromosomes or pairs.

The chromosomes change their form in the interkinesis, becoming long spiral threads which shorten on the approach of the homotypic mitosis when the six chromosomes again appear as three pairs showing the same characteristic range of form. The members of these three pairs are distributed by this division so that the nucleus of each pollen grain receives three chromosomes, a short, a long, and a middle-sized element, and these may be recognized in the resting nucleus by three prochromosomes.

A brief examination of the mitoses in the embryo-sac supported the conclusions above outlined.

BRADLEY M. DAVIS.

The Study of Stellar Evolution

An Account of Some Modern Methods of Astrophysical Research

By GEORGE ELLERY HALE

The introduction of photographic methods, the improvement of telescopes, and the rapidly increasing appreciation of the value to astronomy of physical instruments and processes, have revolutionized the observatory. From a simple observing station it has been transformed into a great physical laboratory, where images of the sun and stars are studied with many powerful instruments, and celestial phenomena are experimentally imitated with the aid of electric furnaces and other sources of intense heat. The result has been a great gain in our knowledge of the origin, development, and decay of stars. This books explains in a popular way how the life histories of the sun and stars are investigated. One hundred and four half-tone plates, made from the best astronomical negatives, place before the reader the most recent results of celestial photography in most of its phases.

250 pages, 104 plates, 8vo, cloth; net $4.00, postpaid $4.27

Address Dept. 38

THE UNIVERSITY OF CHICAGO PRESS

CHICAGO **NEW YORK**

Published in Europe by William Wesley and Son, 28 Essex Street, Strand, London, Price, 16s. 6d.

ESSAYS PHILOSOPHICAL AND PSYCHOLOGICAL.

IN HONOR OF WILLIAM JAMES, PROFESSOR IN HARVARD UNIVERSITY BY HIS COLLEAGUES AT COLUMBIA UNIVERSITY

This volume is intended to mark in some degree its authors' sense of Professor James's memorable services in philosophy and psychology, the vitality he has added to those studies, and the encouragement that has flowed from him to colleagues without number. From Prefatory Note.

Philosophical Essays.

The New Realism ..... George Stuart Fullerton
Does Reality possess Practical Character? ..... John Dewey
A Factor in the Genesis of Idealism ..... Wendell T. Bush
Consciousness a Form of Energy ..... Wm. Pepperrell Montague
Perception and Epistemology ..... Frederick J. E. Woodbridge
Substitutionalism ..... C. A. Strong
World-Pictures ..... Walter Boughton Pitkin
Naïve Realism: What Is It? ..... Dickinson S. Miller
Kant and the English Platonists ..... Arthur O. Lovejoy
A Critique of Kant's Ethics ..... Felix Adler
The Abuse of Abstraction in Ethics ..... Herbert Gardiner Lord
Purposive Consistency, the Outline of a Classification of Values ..... G. A. Tawney
The Problem of Method in Mathematics and Philosophy ..... Harold Chapman Brown

Psychological Essays.

Pragmatism in Æsthetics ..... Kate Gordon
The Consciousness of Relation ..... R. S. Woodworth
On the Variability of Individual Judgment ..... Frederic Lyman Wells
The Validity of Judgments of Character ..... Naomi Norsworthy
Reactions and Perceptions ..... James McKeen Cattell
A Pragmatic Substitute for Free Will ..... Edward L. Thorndike

With Photograph of Professor James.

LONGMANS, GREEN & COMPANY. **91 Fifth Avenue, New York City**

The American Naturalist

A Monthly Journal, established in 1867, Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Organic Evolution and Heredity

CONTENTS OF MARCH NUMBER

Invitation Papers at the Baltimore Meeting of the Botanical Society of America; Darwin Memorial Session:—
Darwin as a Naturalist; Darwin's Work on Cross Pollination in Plants. Professor WILLIAM TRELEASE.
Darwin's Influence upon Plant Geography and Ecology. Professor FREDERIC E. CLEMENTS.
Darwin's Work on Movement in Plants. Professor HERBERT MAULE RICHARDS.
An Examination of Darwin's "Origin of Species" in the Light of Recent Observations and Experiments. Professor EDWIN LINTON.
The Distinction between Development and Heredity in Inbreeding. DR. EDWARD M. EAST.
Breeding Experiments with Rats. Professor T. H. MORGAN.
Shorter Articles and Discussion: The Chub and th e Texas Horn Fly, Dr. ROY L. MOODIE. A New Camel from the Lower Miocene of Nebraska, HAROLD JAMES COOK.
Notes and Literature: *Heredity*—The Chondriosomes as Bearers of the Hereditary Qualities, F. PAYNE. Cultural Bed Mutations in the Potato.

CONTENTS OF THE APRIL NUMBER

Heredity of Hair Color in Man. GERTRUDE C. DAVENPORT and CHARLES C. DAVENPORT.
A Mechanism for Organic Correlation. Professor G. H. PARKER.
Recent Advances in the Study of Vascular Anatomy.
Vascular Anatomy and the Reproductive Structures. Professor JOHN M. COULTER.
The Progress of Plant Anatomy During the Last Decade. Professor EDWARD C. JEFFREY.
Shorter Articles and Correspondence: A Note on the Degree of Accuracy of the Biometric Constants, DR. RAYMOND PEARL. Pure Strains as Artifacts of Breeding. O. F. COOK.
Notes and Literature: *Heredity*—The Nature of "Unit" Characters, DR. W. J. SPILLMAN. *Environment*—DR. FRANK E. LUTZ. *Experimental Zoology*—Hybridology and Gynandromorphism, Professor T. H. MORGAN. *Echinodermata*—Red Sea Crinoids, DR. AUSTIN HOBART CLARK.

CONTENTS OF THE MAY NUMBER

The Categories of Variation. Professor S. J. HOLMES.

The General Entomological Ecology of the Indian Corn Plant. S. A. FORBES.

Notes and Literature: *Biometrics*—Some Recent Studies on Growth. DR. RAYMOND PEARL. *Experimental Zoology*—Cuénot on the Honey Bee, Professor T. H. MORGAN. *The Upholding of Darwin*—Poulton and Plate on Evolution, V. L. K.

CONTENTS OF THE JUNE NUMBER

Heredity and Variation in the Simplest Organisms. Professor H. S. JENNINGS.
The Color Sense of the Honey Bee — Is Conspicuousness an Advantage to Flowers? JOHN H. LOVELL.
Variation in the Number of Seeds per Pod in the Broom, Cytisus scoparius. Doctor J. ARTHUR HARRIS.
Present Problems in Plant Ecology:
The Trend of Ecological Philosophy. Professor HENRY C. COWLES.
The Present Problems of Physiological Plant Ecology. DR. BURTON LIVINGSTON.
Notes and Literature: Notes on Evolution, V. L. K. DeVries's Species and Varieties, DR. GEORGE H. SHULL. *Embryology* — On the Totipotence of the First Two Blastomeres of the Frog's Egg. DR. J. F. MCCLENDON.

CONTENTS OF THE JULY NUMBER

Selection Index Numbers and their Use in Breeding. Dr. RAYMOND PEARL and FRANK M. SURFACE.
A Contribution to the Theory of Orthogenesis. DR. ALEXANDER G. RUTHVEN.
The "Presence and Absence" Hypothesis. DR. GEORGE HARRISON SHULL.
Present Problems in Plant Ecology: Vegetation and Altitude. Professor CHARLES H. SHAW.
Shorter Articles and Correspondence: Pleistocene Swamp Deposits in Virginia. DR. EDWARD W. BERRY.
Notes and Literature: *Heredity*—A Case of Non-Mendelian Heredity. DR. W. J. SPILLMAN.

CONTENTS OF THE AUGUST NUMBER

The New Flora of Krakatau. Professor DOUGLAS HOUGHTON CAMPBELL.
A Male Crayfish with Some Female Organs. Professor E. A. ANDREWS.
Present Problems in Plant Ecology:
Problems of Local Distribution on Arid Regions. Professor VOLNEY M. SPAULDING.
The Relation of the Climatic Factors to Vegetation. Professor EDGAR N. TRANSEAU.
Notes and Literature. Recent Experiments on the Inheritance of Coat Colors in Mice, Professor T. H. MORGAN. Some Experiments in Breeding Slugs. Professor T. D. A. COCKERELL.

Single Number 35 Cents **Yearly Subscription, $4.00**

The NATURALIST will be sent to new subscribers for four months for One Dollar

THE SCIENCE PRESS

Garrison, N. Y. **Sub-Station 84: NEW YORK** **Lancaster, Pa.**

VOL. XLIII, NO. 514 OCTOBER, 1909

THE AMERICAN NATURALIST

A MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

CONTENTS

Page

I. **The Non-muscular Articulations of Crinoids.** AUSTIN HOBART CLARK. . 577

II. **On Some Dinichthyid Armor Plates from the Marcellus Shale.** BURNETT SMITH. 588

III. **Are Species Realities or Concepts only.** Professor J. H. POWERS. . . 598

IV. **Shorter Articles and Discussion:** A Light Weight, Portable Outfit for the Study and Transportation of Ants. EDITH N. BUCKINGHAM. Comparison of Cænolestes with Polyprotodonta and Diprotodonta. PAULINE H. DEDERER 611

V. **Notes and Literature:** *Comparative Psychology* — Bohn's "The Birth of Intelligence": Professor H. S. JENNINGS. *Mammalogy* — Osgood's Revision of the Mice of the Genus Peromyscus, Dr. J. A. ALLEN. Leo Errara, Professor CHARLES E. BESSEY. 619

THE SCIENCE PRESS

LANCASTER, PA. GARRISON, N. Y.

NEW YORK: SUB-STATION 84

The American Naturalist

MSS. intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS

Lancaster, Pa. Garrison, N. Y.

NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

Important New Scientific Books

PUBLISHED BY THE MACMILLAN COMPANY

Botany

The Origin of a Land Flora. A Theory based upon the facts of Alternation. By F. O. BOWER, Sc.D., F.R.S. With numerous illustrations.

Cloth, gilt top, xi+727 pp., illus., index, 8vo, $5.50 net.

NOTE.—A profound study in the morphology of the lowest forms of plants, with special reference to the development of their reproductive systems. The author endeavors to show that the present land flora has originated from an aquatic ancestor, and traces the methods of specialization to the land habit, and the establishment of the forms of the higher plants. A book of the highest importance not only to botanists but to biologists in general.

NEW AND STANDARD HAND-BOOKS ON AGRICULTURE, ETC.

Elements of Agriculture, Southern and Western. By W. C. WELBORN, B.S., M.S., M.P.A.

Cloth, xvi+329 pp., illus., appendix, glossary, index, 12mo, $.75 net.

NOTE.—This is a thoroughly modern treatise on farming as practiced in the Gulf States, from the point of view of the scientific agriculturist. It is adapted to school use, but is of practical service to any farmer in that part of the country. The author is vice-director of the Texas Experiment Station.

Re-issues of the highly valued Hand-Books known as the Garden Craft and Rural Science Series, edited by L. H. BAILEY, of Cornell University, Editor of "Cyclopedia of American Horticulture," "Cyclopedia of American Agriculture," etc.

The Principles of Fruit Growing. By L. H. BAILEY.
Tenth Edition, $1.50 net, by mail $1.66.

Irrigation and Drainage. By F. H. KING.
Fifth Edition, $1.50 net, by mail $1.68.

Principles of Vegetable Gardening. By L. H. BAILEY.
Sixth Edition, $1.50 net, by mail $1.68.

Bush Fruits. By FRED W. CARD.
Fourth Edition, $1.50 net, by mail $1.66.

Fertilizers. By EDWARD B. VOORHEES.
Tenth Edition, $1.25 net, by mail $1.38

Farm Poultry. By GEO. C. WATSON.
Sixth Edition, $1.25 net, by mail $1.42

Published By **The Macmillan Company** 64-66 5th Ave., New York

THE
AMERICAN NATURALIST

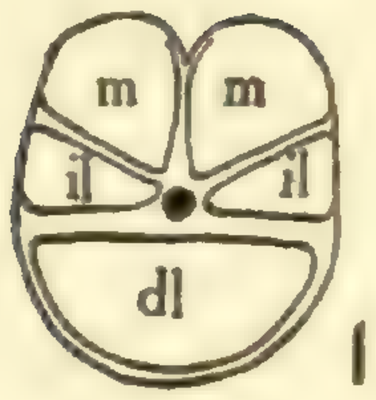
VOL. XLIII *October, 1909* No. 514

THE NON-MUSCULAR ARTICULATIONS OF CRINOIDS

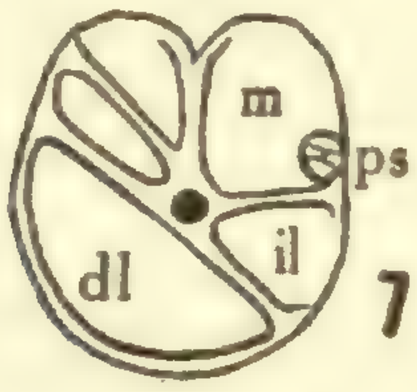
AUSTIN HOBART CLARK

IT has been long known that the non-muscular articulations in the crinoid arm, synarthries or bifascial articulations, and syzygies, have an entirely different effect upon the arm structure than do articulations possessing muscle bundles, straight or oblique muscular articulations. The muscular articulations are composed of three elements (Figs. 1 and 7); (1) the dorsal ligament, bounded ventrally by a strong transverse ridge running across the middle of the joint face, (2) the interarticular ligaments, just ventral to the transverse ridge, occupying triangular areas one on each side of the central canal, and (3) the muscle bundles, occupying two large distally rounded areas, separated by a narrow median ridge or furrow; in straight muscular articulations (Fig. 1) the transverse ridge separating the dorsal ligament fossa from the interarticular ligament fossæ runs at right angles to the dorsoventral axis of the joint face, and the two interarticular ligament fossæ and two muscular fossæ are of equal size, while in oblique muscular articulations (Fig. 7) the transverse ridge is strongly diagonal in position, and the two interarticular ligaments and two muscular fossæ are, on one side crowded, on the other drawn out, and therefore unequal.

The non-muscular articulations (Figs. 5 and 11) are

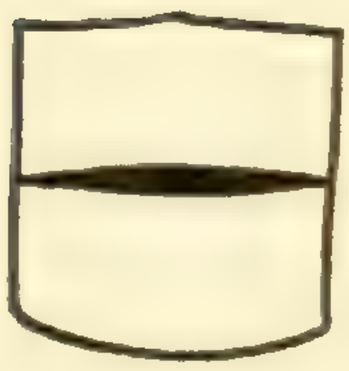


1



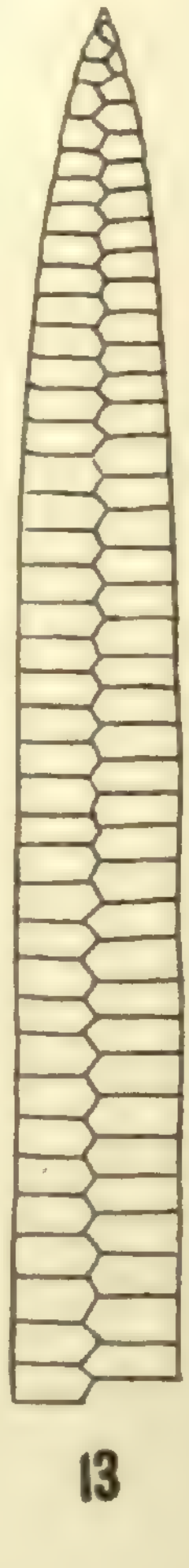
7

14

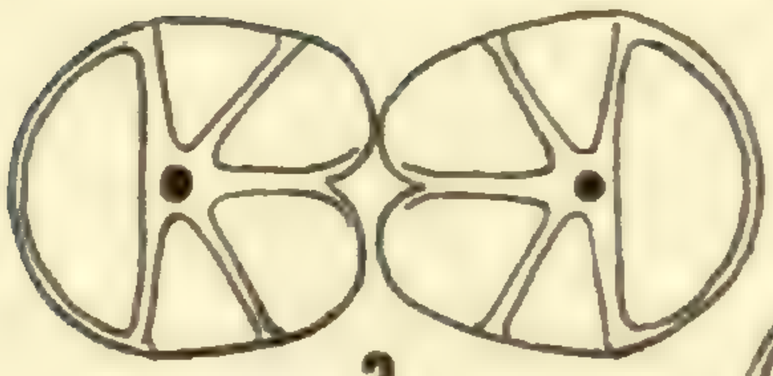


2

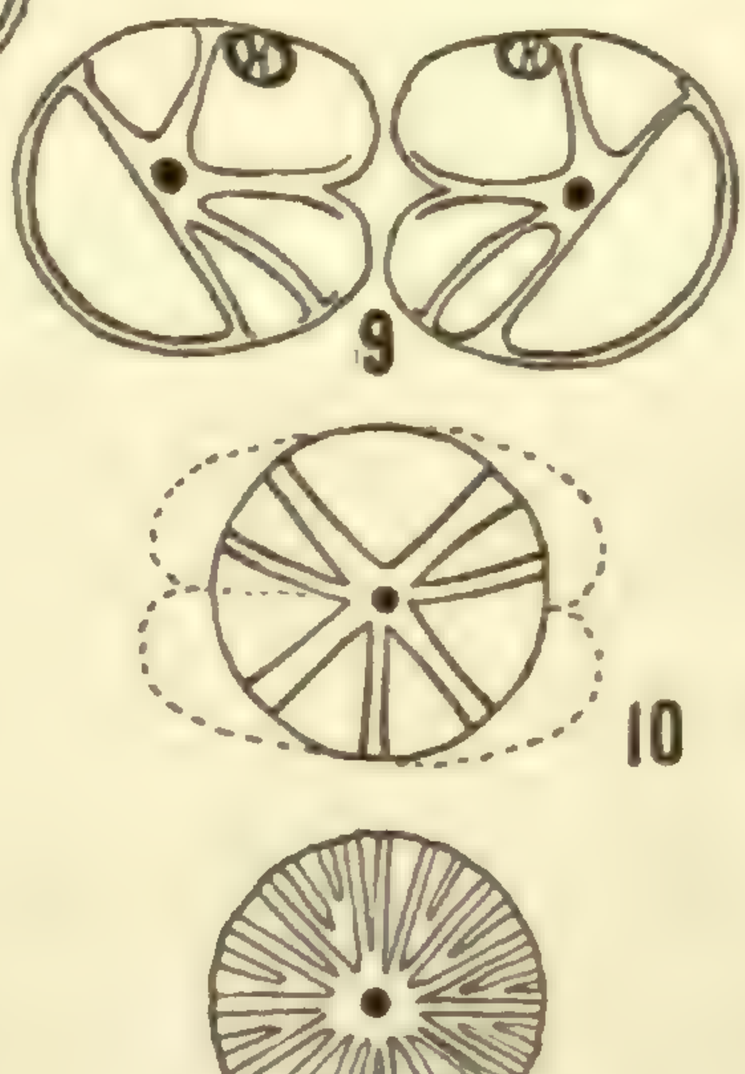
8



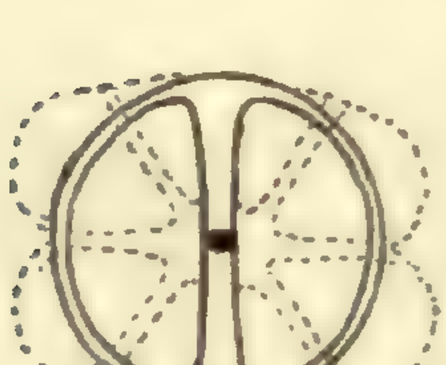
13



3



9

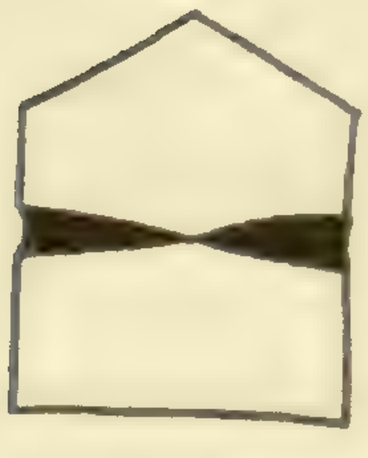


4

10

5

11



6

12

FIG. 1. Articular Face of a Straight Muscular Articulation: *m*, muscular fossæ; *il*, interarticular ligament fossæ; *dl*, dorsal ligament fossæ.

FIG. 2. Dorsal External View of a Straight Muscular Articulation between two Ossicles-

FIG. 3. Two straight Muscular Articulations revolved through an Angle of 90°.

FIG. 4. The same, superposed so that their central Canals Coincide.

FIG. 5. A synarthry.

FIG. 6. External Dorsal View of a Synarthry between two ossicles.

FIG. 7. Articular Face of an Oblique Muscular Articulation; *m*, muscular fossa; *ps*, pinnule socket; *il*, interarticular ligament fossa; *dl*, dorsal ligament fossa.

bound together with ligament fibers similar to those of the dorsal ligament of muscular articulations; in synarthries (Fig. 5) these fibers are segregated into two large bundles lateral in position, separated by a dorsoventral ridge across the joint face; in syzygies (Fig. 11) the fibers are scattered over the whole joint surface, which is broken up into alternating ridges and furrows radiating outward from the central canal, which may, in certain of the more specialized forms, such as the Pentacrinitidæ, become obsolete except about the periphery of the joint face.

Muscular articulations are often doubled, thus forming an axillary from which two arms arise; this never happens in the case of non-muscular articulations; moreover, muscular articulations are primarily pinnulate, the pinnule arising from a pinnule socket in the proximal outer part of one of the muscular fossæ. The difference between straight and oblique muscular articulations was originally a difference in pinnulation. In the most primitive type of crinoid arm found among the recent forms, occurring in the family Pentametrocrinidæ, we find the following sequence of articulations: (1) straight muscular, uniting the radial to the first post-radial joint, (2) synarthry, uniting the first two post-radial joints, (3) oblique muscular, uniting the second and third post-radial joints; all the succeeding articulations are oblique muscular, except for the interpolation of occasional syzygies. The first oblique muscular articulation bears the first pinnule; the addition of a pinnule socket on one side of the joint face causes a certain amount of crowding, and a conse-

FIG. 8. External Dorsal View of three oblique Muscular Articulations.

FIG. 9. Two Oblique Muscular Articulations revolved through an angle of 90°.

FIG. 10. The same, superposed so that their central Canals Coincide.

FIG. 11. A Syzygy.

FIG. 12. External Dorsal View of a Syzygy between two Ossicles; note how its course across the arm is the mean of the course of the preceding and succeeding oblique muscular articulations.

FIG. 13. A Biserial Crinoid Arm.

FIG. 14. A Monoserial Crinoid Arm, showing the triangular joints, the indices of an ancestral biserial arrangement.

quent depression dorsally of that half of the transverse ridge, which is compensated by a ventral depression of the opposite half; this alteration in one half of the transverse ridge is a necessary consequent of any alteration in direction of the other half, for the transverse ridge is the fulcrum upon which the bending of the arm occurs, and the fulcrum must always be a straight line to admit of any motion at all. Although primarily pinnulate, in certain rare cases oblique muscular articulations are sometimes found non-pinnulate, as in *Atelecrinus, Hypalometra, Cyllometra,* and *Perometra;* but this is a purely secondary condition, and one peculiarly prone to reversion, showing it to be somewhat unstable. In all cases, the position of the first oblique muscular articulation is the second articulation beyond the last straight muscular articulation of the arm. The oblique muscular articulations always alternate in the position of their diagonal transverse ridges, and the transverse ridges of succeeding joints form angles of approximately 90° with each other; therefore, a single brachial has proximally an articular face with the transverse ridge from a left ventro-lateral to a right dorso-lateral point, and distally an articular face with the transverse ridge running from a left dorso-lateral to a right ventro-lateral position. The pinnule socket always occurs on the side on which the end of the transverse ridge is dorso-lateral in position; hence, pinnules occur on alternate sides of the arm at succeeding articulations. In reality, of course, the alternation of the pinnules is the fundamental cause of the alternation in the direction of the transverse ridge, but, from the absence of pinnules on oblique muscular articulations in certain recent types, it is more convenient to speak of it as if the reverse were the case.

Non-muscular articulations are never doubled, are never pinnulate, and moreover, never affect the pinnulation in any way; the pinnule on the next succeeding muscular articulation is on the opposite side from that of the preceding muscular articulation, just as if the non-mus-

cular articulation were not there, but the two joints connected by it merely a single joint.

Of the non-muscular articulations, the synarthry occurs in the proximal part of the arm, the last synarthry immediately preceding the first oblique muscular, and immediately succeeding the last straight muscular articulation; all the non-muscular articulations succeeding the first oblique muscular articulation are always syzygies. In the simple arms of the Pentametrocrinidæ we find a straight muscular articulation, a synarthry, and then a series of oblique muscular articulations, interspersed with occasional syzygies. In this family the first brachial immediately follows the radial; but in all the other comatulids and in the recent species of the Pentacrinitidæ (except in the genus *Metacrinus*) the first brachial is separated from the radial by one or more interpolated division series, each composed of a reduplication of the first two brachials interpolated between the primitive first brachial and the radial. In these, however, the structure is the same; a series of synarthries alternating with straight muscular articulations occurs up to the first oblique muscular articulation, beyond which are found only oblique muscular articulations and syzygies. This is the primitive arrangement of the comatulid and pentacrinite arm, no matter how many times division may occur; but in certain specialized types, as *Endoxocrinus* and the Zygometridæ, one or more of the synarthries may be secondarily replaced by syzygies.

From the above discussion it is evident that (1) non-muscular articulations are morphologically radically different from muscular articulations; and (2) that there is a distinct interrelation between the two types of muscular articulations and the two types of non-muscular articulations; that is, that proximal to the first oblique muscular articulation *only straight muscular articulations and synarthries are found*, while distal to the first oblique muscular articulation occur *only oblique muscular*

articulations and syzygies; moreover, the synarthries always alternate with the straight muscular articulations, while the occurrence of the syzygies is more or less, and often very, irregular.

Bearing these facts in mind, we are able to reach a definite concept of the morphological significance of the synarthries and syzygies, in terms of straight and oblique muscular articulations. We have seen that the transverse ridges of succeeding oblique muscular articulations are always approximately at right angles to each other, and we may from this infer a fundamentally alternate position in all muscular articulations. The first articulation, uniting the radial to the first post-radial joint is straight muscular, with the transverse ridge at right angles to the dorso-ventral axis of the joint faces; according to what we found to be the case in oblique muscular articulations, the next articulation should be straight muscular, with the transverse ridge at right angles to that of the first, or coinciding with the dorso-ventral axis; but such an arrangement would leave the muscles and the interarticular ligaments on one side of the arm, and the dorsal ligament on the other, which would be manifestly absurd; but we actually find a transverse ridge running along the dorso-ventral axis of the joint face, with on either side of it a dorsal ligament bundle, *in every way the same as the dorsal ligament bundle of the preceding straight muscular articulation.* The synarthry, then, appears to consist fundamentally of the dorsal ligaments of *two* straight muscular articulations, abutting upon a common transverse ridge, which is at right angles to the transverse ridge of the preceding straight muscular articulation (Figs. 3 and 4). Not only does the microscopical comparison of the two individual muscle bundles of the synarthry with the dorsal ligament bundle of the straight muscular articulation bear out this interpretation of the origin of the synarthry, but the morphological effect of the synarthy upon the arm structure is at once explained. Non-muscular articulations never bear pin-

nules; pinnules are borne upon the muscular fossæ of muscular articulations; in the projection of one straight muscular articulation upon another to form the synarthry, the interarticular ligaments and the muscles are cut out, and only the dorsal ligament remains; with the elimination of the muscular fossæ, the pinnule sockets are lost; hence, synarthries can never bear pinnules, as the pinnule-bearing element of the articular face is omitted from their composition. Synarthries never affect the pinnulation; if a pinnule be borne on the left side of a straight muscular articulation preceding a synarthry, the pinnule on the next succeeding straight muscular articulation will invariably be upon the right side. A synarthry is primarily composed of two coalesced succeeding muscular articulations, one of which potentially bears a pinnule upon the opposite side from that of the other; these two primitive elements of the synarthry, being of exactly opposite tendencies in respect to their pinnules, counteract each other upon being merged, and hence we find the synarthry neutral in regard to pinnule arrangement; the synarthry possessing primarily (morphologically) *two* pinnules, the next following muscular articulation has its pinnule thrown to the opposite side of the arm from that on the muscular articulation preceding. Thus a synarthry, in reality, instead of having no effect upon the pinnule arrangement, has a double effect (though with the same result), throwing the pinnule to one side of the arm and back again within the compass of a single articulation.

Muscular articulations are frequently doubled, thus forming an axillary from which two similar arms arise; synarthries are never doubled; they are already double articulations, and a further doubling would be equivalent to a quadrupling of muscular articulations.

The syzygy is different from the synarthry only because it is formed from two *oblique* instead of *straight* muscular articulations (Figs. 9 and 10). A rotation of a straight muscular articulation through 90° brings the

transverse ridge into the dorso-ventral axis; hence, the transverse ridges of the two primitive straight muscular articulations coincide, and remain unchanged in the resultant synarthry; a rotation of two succeeding oblique muscular articulations 90° will, as their transverse ridges are already at right angles to each other, keep them in the same relative position; projecting one of them upon the other, the two transverse ridges form a right-angled cross; since the muscles and interarticular ligaments, being recessive when compared with the dominant dorsal ligament, disappear, we get an articulation consisting of a mass of dorsal ligament fiber crossed by radiating ridges. This crossing of the two fulcra upon a single joint face effectually prevents any movement at the articulation, and thus we get the primitive syzygy. The multiplication of the radiating ridges is without doubt a secondary development, though possibly four of them represent the distal edges of the interarticular ligament fossæ. The interpretation of a syzygy as a combination of the ligaments of two oblique muscular articulations explains the uniformly single condition of the syzygy, the absence of pinnules, and the neutrality of the syzygy in regard to pinnulation, this being brought about in the same way as in the synarthry, the resultant of two straight muscular articulations.

The interpretation of synarthries and syzygies just proposed involves a doubling up and merging together of the elements of two muscular articulations. This, it might well be argued, would be an occurrence improbable in the extreme in a linear series of joints and articulations. The ambulacral system of echinoderms, however, is composed primarily of a double series of joints, plates or whatever the elements may be, the first element alone being single. Thus in the urchins the oculars stand at the head of the double row of plates composing the ambulacra; and in the crinoids the radials stand at the end of an ambulacral system composed, in many genera, of two rows of plates, side by side, in biserial arrange-

ment. The similarity is even more striking; in the urchins new plates are added only between the ocular and the next succeeding plate, and it has been urged that the addition of new plates only at the ends of the arms in crinoids constitutes an important morphological difference between the ambulacral systems of the two groups. I have recently shown, however, that in almost all the recent crinoids (and similarly in many of the fossils) plates are added between the radials and next following joints (interpolated division series) just as in the urchins; the process of interpolation is different, but the result is morphologically identical in the two cases. J. S. Miller in 1821 first called attention to the similarity of a crinoid to an inverted *Cidaris*, but I believe the resemblance between the ambulacral systems of the two are closer and more fundamental than was supposed either by Lovén or by Carpenter. All the recent and most of the fossil crinoids have uniserial arms, but the brachials are always, at least in the proximal third of the arm, triangular or obliquely wedge shaped, a condition which is most pronounced in the young. Now, applying Jackson's law of "localized stages," we may assume in the crinoid arm that the joints which are ontogenetically the oldest are phylogenetically the oldest also; and we should thus be led to look for ancestral characters toward the arm bases. Here we find joints much more triangular than farther out, the distal and proximal ends being very oblique; hence we should infer an ancestry of forms with sharply triangular brachials; but certain comatulids go even farther in the proximal third of the arm, the brachials having borders so oblique that the inner apices of the triangles do not reach to the opposite border of the arm. Judging from recent forms alone, then (to say nothing of the fossils), we are irresistibly led to the conclusion that the biserial condition is the fundamental condition of the crinoid arm, just as the double row of ambulacral plates is the fundamental condition in the urchins, and that the monoserial arrangement is purely secondary,

an adaptation to special conditions of existence. The change from a biserial to a monoserial arrangement in the crinoids is merely a matter of an elongation of the arm, and a slipping in of the joints in one series between those of the other (Fig. 9). It has been suggested that *Encrinus, Platycrinus* and the other biserial crinoid genera are derived from monoserial ancestors because the new joints as they are formed at the arm tip are always monoserial in arrangement; but apart from the mechanical difficulties in the way of biserial termination to a free arm like that of the crinoids, we find that almost the same is true in the urchins; plates are added one by one abutting upon the median ambulacral line just behind the oculars, which move out by lateral growth first to one side then to the other, just as the monoserial plates at the tip of a *Platycrinus* or *Encrinus* arm, on increasing in size, more laterally first to one series, then to the other; the supposedly monoserial tip in biserial crinoid genera, therefore, appears to be, in reality not monoserial at all, any more than the proximal (post ocular) portion of the ambulacra in the urchins is monoserial.

The slipping in of the two series of joints in the biserial crinoid arm in the transition from a biserial to a monoserial condition undoubtedly first gave rise to synarthries and syzygies, the former originating from the coalescence of two straight muscular articulations, the latter from the coalescence of two oblique muscular articulations. I have been unable to study the joint faces of crinoids of the biserial type, and therefore have not traced the process, but, judging from the data at hand there seems to be much in favor of such an origin for spnarthries and for syzygies, and I hope to be able to adduce additional evidence in support of it in the future. A study of the ontogeny of *Antedon* does not help us, for in that type the synarthry and the syzygy are ontogenetically older than the beginnings of the deposition of calcareous matter, and the synarthry between the first two postradial joints is ontologically nearly or quite as

old as the phylogenetically much more primitive straight muscular articulation between the radial and the first postradial joint, and ontologically older than the straight muscular articulation succeeding it. Neither can we hope for any light when we know the embryology of the Pentacrinitidæ, for the early stages of the Pentacrinitidæ are undoubtedly practically the same as those of the comatulids, the only tangible difference in the adults being an enormous increase in the number of the short discoidal joints occurring at the top of the *Antedon* stem, and (of secondary importance) the retention of the stem. I have only been able to examine a very few fossils in regard to the interbrachial articulations; the results of my study of *Vintacrinus* have already been published; *Pentacrinites* (*"Extracrinus"*) is exactly like *Isocrinus* (restricted, *i. e.*, excluding *Endoxocrinus*) except for the small detail of the heterotomous instead of dichotomous condition of the extraneous division series, and *Marsupites* is exactly like *Antedon*, even in the position of the proximal syzygies; but I am convinced that a detailed and careful study of the articulations and articular faces of the joints in the fossil crinoids is one of the best lines of procedure in the elucidation of their systematic relations.

ON SOME DINICHTHYID ARMOR PLATES FROM THE MARCELLUS SHALE

BURNETT SMITH
SYRACUSE UNIVERSITY

INTRODUCTION

THOUGH Devonian beds in many parts of the world frequently furnish an abundance of piscine fossils, this is not the case with their cotemporaneous deposits of the state of New York. In this region every bit of evidence which may add to our knowledge of the anatomy, geographical distribution and geological range of the Devonian members of the class may at any time become of interest, for amid profuse invertebrate faunas the fish remains are usually rare, inconspicuous and fragmentary.

It is, therefore, believed that a recent find of the complete ventral armor[1] (together with some other bones) of a small species of Dinichthys is worthy of some notice in spite of the fact that the preservation leaves much to be desired and also that any interpretations based on the material are apt to prove untenable when more complete and more perfectly preserved specimens are brought to light.

DESCRIPTION OF THE FIGURES

The specimen in question came from the concretion zone of the Marcellus Shale in the vicinity of Syracuse, N. Y., and was collected by the writer in the summer of 1908. Its geological horizon is not determinable with absolute certainty, but it lies not far (within fifteen feet at most) above the top of the Agoniatites Limestone, which in this section is itself confined to the lower fifteen

[1] The writer must express his indebtedness to Dr. Louis Hussakof and to Dr. Charles R. Eastman, both of whom generously examined the photographs of this specimen and gave him invaluable assistance in the interpretation of its osteology.

or twenty feet of the Marcellus Shale formation. The geological position of the specimen together with its size and the character of its external ornamentation points strongly to its identity with *Dinichthys halmodeus* (Clarke).[2] It is realized perfectly that this identification may prove incorrect but for purposes of convenience the specimen will throughout this paper be considered as belonging to that species.

The fossil occurs as a probable nucleus for one of the large concretions, though its position in the mass is excentral. It has been laid bare by the removal of a part of the concretion and apparently has been subjected to weathering for a considerable time. This has resulted in the loss of nearly all of the external ornament, only one or two small patches of bone exhibiting the superficial tuberculation. How much of the skeleton has disappeared with the missing portion of the concretion it is impossible to say, for diligent search has failed to reveal its presence in the immediate neighborhood.

The concretions at this horizon are crossed by at least two sets of irregular planes of fracture which have been infiltrated with barite, calcite and other minerals. We, therefore, have (1) lines crossing the specimen which are incident to the formation of the concretion itself, (2) lines of fracture in the fossil which are independent of structural features and (3) the lines which mark the boundaries of the different bones. This fact is mentioned here in order to call attention to the many lines in the accompanying photograph (Fig. 1) which must be distinguished from those which represent organic structures.

As stated before, the parts preserved are: (1) the nearly complete ventral armor with its elements in natural association and (2) other scattered bones among which a postero-dorsolateral and an antero-dorsolateral stand out conspicuously (see Figs. 1 and 2).

The Ventral Shield.—In the median region the antero-

[2] *Coccosteus* (?) *halmodeus* Clarke. John M. Clarke. New and Rare Species of Fossils from the Horizons of the Livonia Salt Shaft. Report State Geologist, N. Y., 1893, p. 161.

ventromedian is well preserved posteriorly, but its anterior portion has been broken away. The impression of this missing part is, however, well preserved on the surface of the matrix and there is no difficulty in restoring the outline of this plate on its forward margin. Posteriorly it meets the postero-ventromedian, the limits

FIG. 1. *Diniehthys halmodeus* (?) (Clarke). Photograph (not retouched) of the ventral shield with associated bones. The long axis of the elliptical surface on which the specimen is exposed measures about 34 cm.

of the two plates being indicated by a curved line whose convex side is directed forward. The postero-ventromedian is clearly outlined, though its surface has been considerably crushed. The antero-ventrolaterals border the two median plates on either side. It is impossible

to make out the exact limits of their inner margins on account of the weathering to which they have been subjected. They lie in a plane higher (more ventral anatomically) than the median plates and undoubtedly overlapped them slightly. On the posterior lateral borders

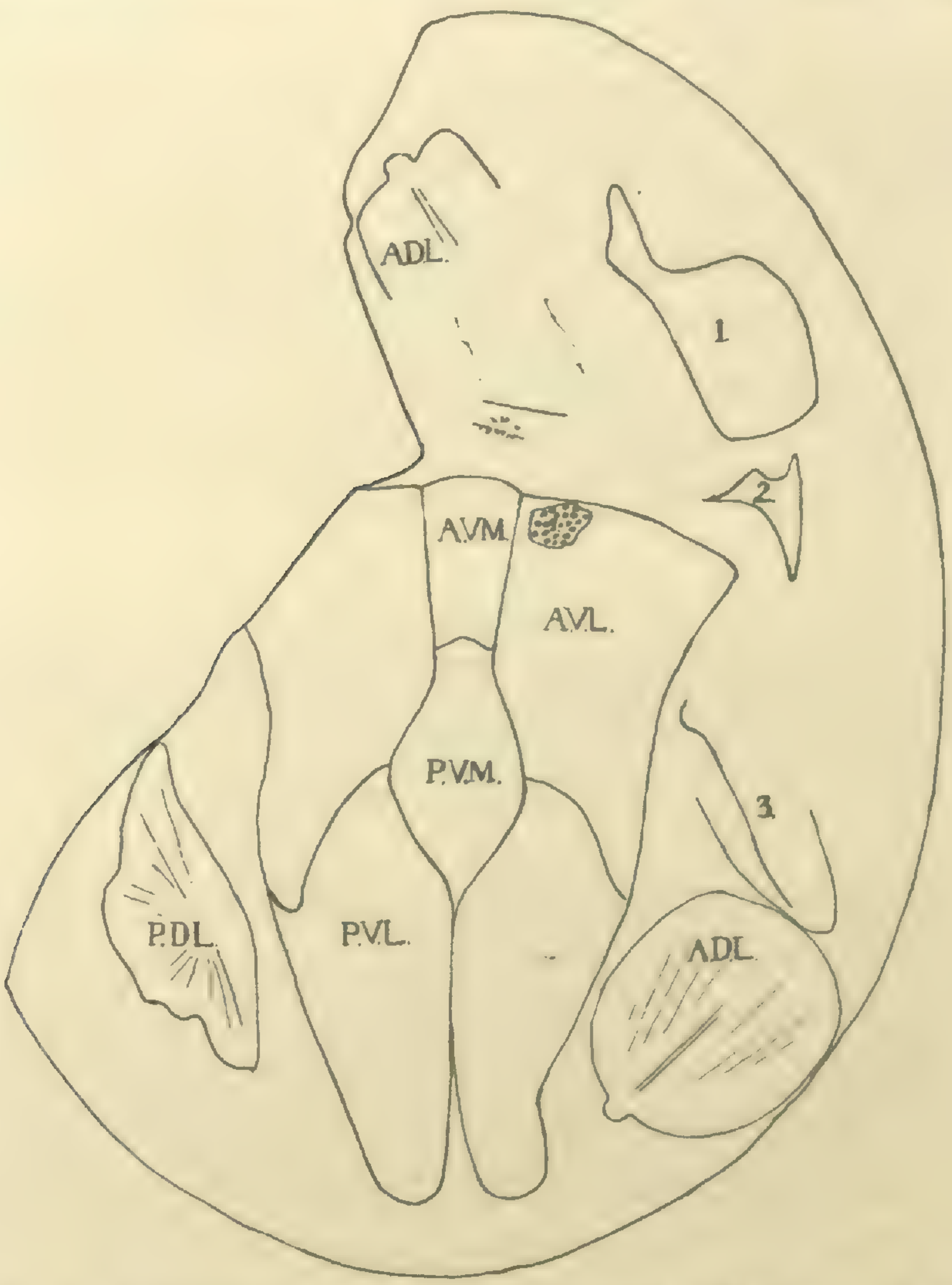


FIG. 2. *D. halmodeus* (?) (Clarke). Drawing made from a tracing of the photograph shown in Fig. 1. *AVM*, antero-ventromedian; *PVM*, postero-ventromedian; *AVL*, antero-ventrolateral; *PVL*, postero-ventrolateral; *PDL*, postero-dorsolateral; *ADL*, antero-dorsolateral; 1, suborbital?; 2, antero-supero-gnathal?; 3, possibly a fragment of the dorsomedian.

of the postero-ventromedian lie the two postero-ventrolaterals. The inner margins of these plates are also hard to delimit. They were overlapped by the antero-ventrolaterals, for they lie at a lower (anatomically more dorsal) plane. The inner margins of all four of the lateral plates

are believed to have been broken or to have weathered away. If this is the case we have exposed the actual lateral outlines of the two median plates. The shape of the entire ventral shield is quite accurately indicated by the outer margins of its constituent plates in spite of fracturing and some displacement. The left antero-ventrolateral still retains a small patch of the exterior surface showing a tuberculation similar to that of a Dinicthyid cranium from Manlius, N. Y., which has been referred by Eastman to *D. halmodeus*.[3] A few obscure tubercles are also present on the left postero-ventrolateral. As exhibited in this specimen the two median plates appear to be quite flat. The antero-ventrolaterals are much crushed, but apparently were slightly convex on their ventral surfaces. The postero-ventrolaterals show convexity on their outer or ventral surfaces.

Bones without the Ventral Shield.—The most conspicuous of these are the postero-dorsolateral and the antero-dorsolateral. The former of these is flat, and though it is much weathered, it appears to furnish us with about the outline of the original plate. The latter is decidedly convex and though much weathered it shows the articular projection and the canal.

Above (forward of) the ventral shield is a confused mass of bones, some of them exhibiting sharp tooth-like denticles, while beyond this again is another poorly preserved antero-dorsolateral exhibiting both the canal and the articular projection. No cranial plates can be made out with certainty, though the bone marked *1* in Fig. 2 might be interpreted as a suborbital, while at *2* is a bone suggesting an antero-supero-gnathal.

COMPARISON WITH OTHER SPECIMENS

As far as the author knows, only two other specimens of Dinichthys with the ventral armor plates in natural association have been recorded. The first specimen was

[3] *N. Y. State Museum Memoir*, 10, p. 128, pl. 10.

described by Von Koenen[4] and referred with doubt to *D. minor*. In this case the material was too poorly preserved to admit of the exact determination of the different bones. In the second specimen the preservation is quite satisfactory and we are indebted to Dr. Eastman[5] for its description. He has referred it tentatively to

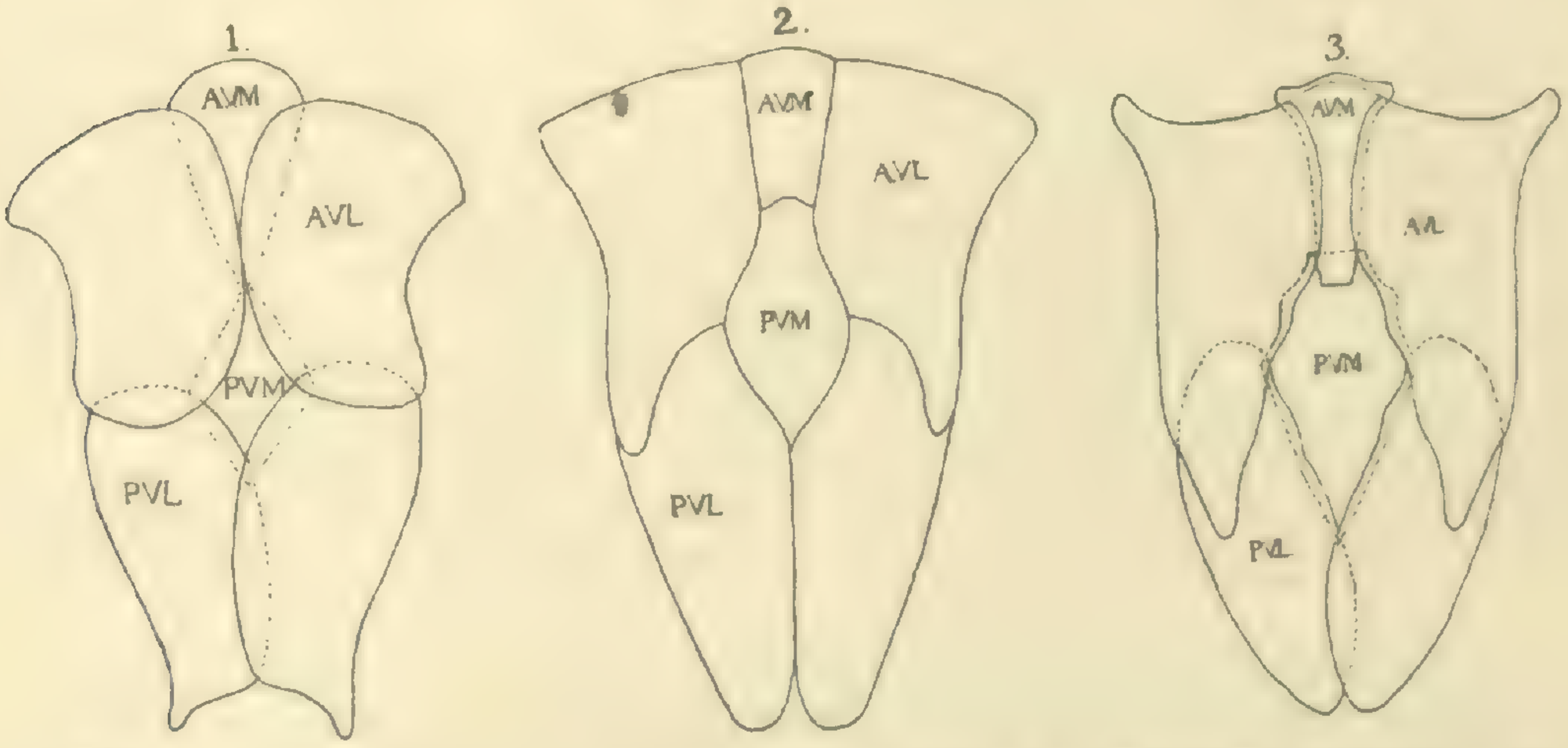


FIG. 3. 1, restoration of the ventral shield of *Coccosteus decipiens* Ag. (modified from Smith Woodward). 2, restoration of the ventral shield of *Dinichthys halmodeus* (?) (Clarke), no attempt being made to indicate overlap. 3, restoration of the ventral shield of *D. newberryi* (?) Clarke (after Eastman). Bones lettered as in Fig. 2.

D. newberryi Clarke. This latter example shows all six of the ventral plates but little removed from the original position. In his restoration Dr. Eastman illustrates the conditions of overlap and brings the bones into the positions which it is believed they occupied in life.

Comparing now (Fig. 3) the restoration of *D. newberryi* (?) with that here regarded as *D. halmodeus* it will be seen that in each case the antero-ventrolateral overlaps the postero-ventrolateral and that all four ventro-laterals overlap the two median plates. When, however, the relations of the two medians are considered we are unable to carry the comparison farther. In *D.*

[4] A. von Koenen. Ueber einige Fischreste des norddeutschen und böhmischen Devons. *Abhandl. K. Gesell. Wissensch. Göttingen*, Vol. XL, pp. 1–37, Plates I–IV, 1895.

[5] C. R. Eastman. On the Relation of Certain Plates in the Dinichthyids. *Bull. Mus. Comp. Zool. Harvard*, Vol. XXXI, October, 1897, pp. 26 and 27, Plate I, fig. 2 and Plate IV.

newberryi (?) the antero-ventromedian overlaps the postero-ventromedian. In the present specimen we can not prove that some overlap did not occur, for the point of junction is much eroded. We can, however, say that no such overlap is indicated and that the two plates appear to be separated by a thin curved suture which is convex anteriorly and concave posteriorly.

When the postero-ventrolaterals are compared with those of *D. newberryi* (?) the general outlines and proportions exhibit great similarity, but this is not the case with the antero-ventrolaterals. In these plates not only is there an apparent difference in the posterior overlapping margins, but the anterior lateral projection is turned posteriorly and not anteriorly as in *D. newberryi* (?). This gives the entire front margin of the ventral shield an evenly convex outline quite different from the bow-shaped line shown by *D. newberryi* (?) and in Hussakof's[6] restoration of *D. curtus*. As a whole the ventral shield exhibits general relations of length to breadth not unlike that of *D. newberryi* (?) but is proportionately much broader and stouter than the restored plastron of *D. curtus* to which reference has been made.

COMPARISON WITH COCCOSTEUS

All authorities on the Arthrodira have united in assigning to *Dinichthys halmodeus* a primitive position among American Dinichthyids and the species is regarded as having diverged only slightly from the ancestral genus Coccosteus. These relationships have been made out by studies on the cranium, the infero-gnathals and on the dorsal body plates.

If then the specimen here considered is indeed specifically identical with *D. halmodeus* we have further confirmation of the practically intermediate position which the species holds between Coccosteus on the one hand and the highly specialized species of Dinichthys on the other.

[6] L. Hussakof. On the Structure of Two Imperfectly Known Dinichthyids. *Bull. Am. Mus. Nat. Hist.*, Vol. XXI, Art. XXV, p. 412.

That the ventral armor of the present specimen belonged to a primitive type is shown: (1) by the fact that the antero-ventromedian and postero-ventromedian are not fused as in such specialized forms as *D. terrelli*[7] and (2) by the fact that the anterior lateral angles of the antero-ventrolaterals are directed posteriorly giving this portion of the ventral shield an outline similar to that of Coccosteus (see Fig. 3).

The fact that the antero- and postero-ventromedians are united by suture and not merely touching or even separate shows an advance from the condition of these elements in Coccosteus, but taking the sum of the characters in the ventral shield we have, on the whole, a closer approximation to this latter genus than to Dinichthys.

Distribution of Dinichthys in the New York Province

In his recent memoir[8] Dr. Eastman lists eight species of *Dinichthys* as occurring in the Devonian of the New York-Pennsylvania Province. Of these six are confined to the upper Devonian, that is, they are found only above the top of the Hamilton shales. Of these, three at least are common to both the New York-Pennsylvania and the Ohio province, while three appear to be restricted to the New York-Pennsylvania province. The Middle Devonian yields but two definite species, *D. lincolni* Claypole and *D. halmodeus* (Clarke). Both are, as far as known, restricted to the Marcellus division of the Middle Devonian. *D. lincolni* is known by a single tooth found in the upper part of the Marcellus Shale twenty-five feet below the basal limestone of the Hamilton. *D. halmodeus* is, according to the same authority, known by three specimens: (1) the type cranium, (2) a dorsomedian plate associated with the type cranium and possibly belonging to the same individual and (3) a cranial fragment. The

[7] See Hussakof's figures, *Mem. Am. Mus. Nat. Hist.*, Vol. IX, pt. III, p. 139.

[8] ***N. Y. State Mus. Mem.*, 10, 1907.**

type material is reported by its original describer as having come from the Livonia salt shaft, Livingston County, N. Y., and its geological horizon is about forty feet above the base of the Marcellus Shale. It lies just below the Stafford Limestone bed of the Marcellus in a black shale and its associates make a typically Marcellus assemblage. Among them are such invertebrates as *Orthoceras subulatum, Styliolina fissurella, Chonetes mucronatus, Leiopteria lævis* and *Leiorhynchus limitaris*.[9] The cranial fragment figured by Dr. Eastman[10] is reported as having come from the Agoniatites Limestone, Hendrick's Ledge, west of Manlius, Onondaga County, N. Y.

The Agoniatites Limestone in Onondaga County lies about thirteen feet above the base of the Marcellus formation, is about two and one half feet thick and is both underlaid and overlaid by the black friable Marcellus shales.[11] The specimen which has been the subject of this brief paper was found in a limy concretion from the upper black shale above the Agoniatites Limestone and probably within ten feet of it. At this point both the shales and the concretions are alike very poor in fossils, none having been found in the shale and a single Ichthyodorulite being the only yield from an examination of many other concretions.

From the evidence of stratigraphy it appears that the limestone lentils of the Marcellus shales are the expressions of changing geographical conditions and invading faunas.[12] They are not everywhere at the same geological horizons with relation to the base of the Marcellus, and as they represent invasions the limestone in one locality may be cotemporaneous with shale in a different

[9] D. D. Luther. *Report on the Livonia Salt Shaft.* Rep. State Geol. N. Y., 1893, p. 81.

[10] *New York State Mus. Mem.*, 10, pl. 10.

[11] John M. Clarke. Marcellus Limestone of Central and Western New York and their Faunas. *N. Y. State Mus. Bull.*, 49.

[12] *N. Y. State Mus. Bull.*, 82, p. 43. The Agoniatites Limestone does not lie between the Marcellus and Cardiff shales as Dr. Eastman has inadvertently stated on p. 129, *N. Y. State Mus. Mem.*, 10.

locality. These limestones then give us the history of areas in the old Marcellus sea which were covered from time to time by invading faunas. It is natural therefore that we should find a species of Dinichthys probably one of the most mobile animals of the time associated: (1) in one locality with the large cephalopods of the Agoniatites Limestone, (2) in another with the small brachiopods and pelecypods of the typical black shale and probably not far from an area occupied by the Stafford fauna and (3) in the unfossiliferous black shale from which the present specimen came.

In his paper cited above Dr. Clarke brings out evidence to show that the Agoniatites Limestone and some of the lower Marcellus black shale in central and eastern New York is the time equivalent of some of the upper Onondaga of the western portion of the state. This lends a peculiar interest to the Onondaga County specimens of *D. halmodeus* which coming as they do from the lower Marcellus lived in a muddy portion of the great New York embayment at no great distance from an area to the west in which Onondaga Limestone conditions prevailed. It is therefore not unreasonable to expect that *D. halmodeus* or some very closely related form may in time be found in the upper Onondaga deposits of this latter region.

ARE SPECIES REALITIES OR CONCEPTS ONLY?[1]

PROFESSOR J. H. POWERS
UNIVERSITY OF NEBRASKA

IN the AMERICAN NATURALIST for April, 1908, there appeared the reprint of some remarkable papers, constituting a symposium by the greater botanists of the country on "Some Aspects of the Species Question."

The attitudes taken toward questions of the nature and reality of species were, on the whole, tentative and questioning. But the opening paper presents, with the utmost lucidity and startling positiveness, a definite conception as to the nature of species: "Species have no actual existence in nature." They are not realities. Individuals alone are real. Species are concepts only, concepts framed by the human mind, and arbitrarily framed withal, for no better reason than its own convenience. Species are compared to spoons, made to fit the human mouth, or the mouth of Linnæus; and until it can be demonstrated—so runs the argument—that this organ has departed appreciably from the typical oral aperture of the great Swede, so long must we continue to fashion our species-spoon-concepts to the exact dimensions of his model.

Now these views, although not wholly new, were a surprise to the writer, both in themselves, in the extremity of their statement and still more in the high authority by which they were supported. Do such things still happen in the botanical world? he queried. Surely no zoologist would for a moment, etc. But hold! "Another Aspect of the Species Question,"[2] by a zoologist this time, and containing the duplicate assertion that many zoologists, "long since reached a satisfactory solution of the species

[1] Studies from the Zoological Laboratory of the University of Nebraska, No. 95.

[2] By Dr. J. A. Allen, NATURALIST for September, 1908.

question by recognition of the fact that species . . . have no real existence, but are merely man-made concepts, purely arbitrary and conventional.''

Is this the dictum of biological science to-day? This by-product of early triumphant Darwinism, with the fear of special creation still upon it, this handy postulate of the sorters of dried birdskins and dried plants, eager to affix tag and title to the whole fauna and flora of a continent—is this the last word of science? Or is it even the limit toward which we are tending? To the writer the reply is unhesitatingly in the negative.

But how refute this proposition of the unreality of species? What reasons have been offered to support it? Unfortunately none. Often suggested in the past, it has been suggested only, and it is now put forward as a self-evident proposition, heavily weighted with authority in lieu of evidence.

Forced by my interest in the subject I have been obliged myself to seek the evidence on both sides of the proposition. I can find but two possible reasons, or rather causes, why species are, or may be, thought unreal. These I wish to state and analyze briefly. Be it fully stated here, however, that I do not for a moment impute these reasons to the minds of scientists whose view of species I am calling into controversy. I find it very difficult to imagine what considerations may have influenced them to the adoption of an hypothesis which seems to me not only fundamentally incorrect but highly injurious to scientific thought and experimentation. I simply assert that, after years of consideration, I can find no other causes for such an assumption and I deem the setting forth of the error in these a useful piece of work.

First of all, then, I think that the unreality of species is frequently assumed, at least by young and careless thinkers, because of what I will term *lapses into uncritical, child consciousness*. This seems a hard saying, and yet nothing is easier than to fall back into methods of thought which we know to be erroneous, but which, just at the times when we feel most certain of ourselves, creep

back upon us because they are the ingrained methods of early uncritical experience.

Now the concept of species is roughly equivalent to the concept of *kind* and this is acquired very early in life. "What's 'at?" asks the child, pointing perhaps to its first sharply perceived bird, a robin, say, in the grass.

"That's a bird, Johnny,—that's a robin."

"What's bird? What's robin?"

"Why a bird is a thing with feathers and wings and that flies. And a robin is a kind of bird. There is a whole lot of them alike, with red on their breasts like that one, and that makes one kind; that makes them robins."

By such experience, such questions and such replies, rapidly extended, the child soon learns the meaning of the word "kind" as it is applied to living things, and later, he transfers this meaning, only a little sharpened, to the word "species."

But those of us who have formed and retained the habit of reviewing our childhood thinking know that these meanings, these concepts of kinds, never seemed wholly real to us as children, and this *simply because the objects of them were not wholly perceived.* This or that kind of bird, as a group, a totality, a whole, was a great vague somewhat, fading out on all sides where it transcended our actual experience; it was luminous only in the center where actual experience and memory kept is *partially real.* The child ascribes reality to perception, and only semireality to conception. But slowly, in adult life, do we partially free ourselves of the sense of unreality in the objects of our conceptual thought.

In science, however, we certainly should and do learn to test, judge and finally affirm the realities back of our concepts, as well as back of our percepts and simple memory images. We know that unvisited foreign countries are no less real than our own, despite their shadowy vagueness in conception. We ascribe exactly the same reality to the surface of the earth at the south pole that we do to that under our feet, despite that it has never been perceived by man. More still, plurality, multiplicity, per-

plexing as they are to perception and imagination, do not deter us from the ascription of full reality to aggregates. A forest is not less real than a single tree; a swarm of bees is as circumscribed a reality as a single insect. The fauna or flora of an entire continent is surely conceived as a definite objective reality as much as though it were the smallest, the most homogeneous of units. The solar system is a reality as truly as is a single planet; the planet as truly as is the dewdrop; the dewdrop as truly, nay, more truly than is the atom.

I say that in adult life, and especially after thorough scientific training, we correct the naïve error of ascribing reality only to that which is obviously a unit or which has been vividly perceived. But I deem that, beyond question, we are frequently subject to lapses in our thought, lapses into the child consciousness in which the unitary object of perception seems to us the only true reality.

The truth is that if species are denied reality because they are pluralities instead of units, individuals have absolutely no right to a better status. Individuals are pluralities. We may recall President Jordan's humorous refutation of Descartes's celebrated maxim: I think therefore I am. Descartes, said Jordan, had no right to consider himself a unity; he had no right to the singular pronoun. Descartes was an aggregate of cells; these are the active units. He must at least have said: *we* think, therefore, *we* are.

Of course the cells, too, are not really units, but again, are aggregates,—nay, they are aggregates of aggregates of aggregates at least; they are, moreover, in all probability, quite as fluctuating aggregates as is a whole species; so that, finally, if unity is to be the test of reality, the atom itself, or the electron, withal, is absolutely the only reality with which science has to deal. But alas for even this bed rock of reality. It, too, is not even good sand. For scientific theorists tell us, and undoubtedly with truth, that atoms and electrons are purely imaginary creations, hypothetical *x*'s only, by means of which we steady our thought while deciphering the se-

quences of phenomena. Thus the quest for reality along the road of unity lands us in a complete reductio ad absurdum, acceptable possibly to some metaphysicians, but utterly repugnant to the clarified common sense of science.

If this line of thought as to the status of the individual and the species seems unprofitable or pressed too far for the taste of many, let us return to a closely related but more practical consideration which is now a live factor in several working lines of biological science. I refer to the fact that individuals are not units in another sense, —the sense, viz: that they have complex life-histories, and must be so thought of and so spoken of if they are to be treated in a scientific as opposed to a popular sense. An individual animal or plant is not a static but a dynamic thing. It does not all exist at any one time, but exists only as a series or succession of stages, bound together by physical continuity and causation, each preceding stage being an indispensable condition of the next. We can not, thus, by any possibility, handle and "sort" individuals. We can not even perceive them by a simple perceptive process. All we handle, sort or recognize is *specimens;* but these, dead or alive, are but fractions of individuals, signs or suggestions of individuals—non-existent at the moment—but which we then proceed to build up in thought by a long process of that same conceptual nature which we use in arriving at our knowledge of species.

If any one is disposed to gainsay this assertion then let him reply to the question: which, or what, is an individual insect? Is it the fertilized egg or some embryonic stage, some younger or older larva?—is it the pupa or the imago? Possibly some one may reply, "the imago; this is at least the adult individual, and the only reality necessarily considered in dealing with species." But this is surely an unscientific position to hold at the present time, even with regard to the insect; while, if we shift our attention to certain other groups of animals, where growth and to some extent morphological change persist throughout life, even the momentary suggestion of a fixed, stable,

"adult individual" leaves us. The common assumption that there is a fixed, or at least a typical adult state is often more assumption than fact, or if partially true, due to the accident of constant average environmental conditions. Thus the writer was astonished to find that an adult salamander, tallying with every character of the "typical individual" would yet, under favorable environment, betake itself to a new period of development and, larva like, issue therefrom so changed in its supposedly fixed characters of adulthood that nothing short of continuous observation could convince one of its individual identity, or rather continuity with the former phases of itself. To know individuals, then, means to know life-histories. To know life-histories means to save and sift our perceptual experience, and to solidify it, little by little, into concepts quite as complex as are those in and through which we know species themselves.

Yet it is admitted that *individuals are real*, despite this fact that they are made up of phase on phase of shifting though correlated characters, only a part of which we can ever perceive. Why then not admit that species are real? Are they not, likewise, groups of interrelated units (units in the practical working sense of this word)? Are not these units—the individuals—bound together by a common genesis as truly as are the cells of the individual's body? Are not these individuals further united by common interactions—sexual and otherwise—between each other, and between themselves and a common environment? Variable criteria all, it is true, but yet assuredly **real criteria.**

But with these last expressions we have in reality passed to another phase of the subject—from the means by which we know species to the nature of species themselves, and some may well have thought that this transition should have been made immediately. Few, it may be said, are child-like enough to deem species unreal because they are plural and but partially perceived; few are so herbarium-dried, so museum-minded, in thought as to confuse specimens with individuals and deem the latter real

because they may easily be seen and handled. The true reason why some deny reality to species lies, it may be said, not in the nature of our knowledge, but in the nature of the groups of objects which we conveniently designate as species.

Species, it may be stated, are not sharply delimited groups of individuals; species pass into each other and into varieties by insensible gradations. Species are not permanent but transient assemblages of individuals; species change as environment changes. In short, an exaggerated Darwinistic conception of the nature and origin of specific groups may be advanced as a reason for denying them full objective reality. We all know Darwin's conception of species, as accentuated varieties, which were in turn due to accentuation and multiplication of individual differences. Genera, too, he viewed as overgrown species, in which variation and extinction, together with other less obvious causal factors, had led to segregation into minor groups, now, in their turn become species. Species were expanded varieties; genera expanded species.

But certainly this view did not imply, in Darwin's own mind, the non-existence, the unreality of species in nature; though it did imply their derivation by intermediate stages, one from another. If we recall his work definitely we shall remember that he found it necessary to introduce a long and labored analysis to account for the very fact of the sharp segregation between allied species—how it was that characters diverged and genera became broken into compact and contrasting groups rather than remaining a sheer chaos of connected and interlacing forms.

In short, if species are not realities, what aberration of intellect led Darwin to work twenty years collecting facts as to their origin? If species are "concepts only," why did he go to sheep-breeders for light on their nature and genesis instead of to logicians and psychologists? It is these latter who tell us of the nature and origin of concepts. Why did not Darwin entitle his work, "The Non-existence of Species?"

But we have progressed since Darwin, it may be said. I hope we have a little. But have we or have we not progressed toward a conception of animate nature as a chaos of such seething instability that distinctions are essentially arbitrary and boundary lines between groups of forms to be drawn only at the pleasure of the individual with due reference to high authority and venerable tradition? Until I read the luminous article of the leader of the aforesaid symposium I had certainly thought not. I had been led to believe that we were progressing, all in all, in the opposite direction.

I lay claim to no particular knowledge of things botanical. I know there are certain genera of plants where specific and varietal characters are much confused and very possibly undifferentiated. Definite species may in such cases be very possibly undeveloped or degenerate, and therefore non-existent. I remember that in my herbarium days I wondered that botanists would carry their system through, whether or no, and describe species where they themselves plainly doubted their reality. It seemed to me this was following the final advice of the Devil in Faust and building systems of words without meaning. I little dreamed, however, that they would ever go so far as to defend the whole Mephistophelean hypothesis of an essentially arbitrary system of words without objective validity.

Surely some botanists are feeling their way far from this conclusion, when, as for example De Vries, after half a life time of experimentation, formulates a theory of species which is not only that of a real thing in nature, but approaches in definiteness and demarcation to the conception of a chemical compound. Species, for De Vries, are almost chemical compounds. Are chemical compounds—chemical species, so to speak—are they realities, or are they too concepts only?

When I began this paper I had in mind to employ the majority of my space in the presentation and analysis of facts concerning a few species with which I have worked personally and which have been chosen with definite re-

gard to the matter of the light they might throw on the nature and origin, and consequently upon the reality or non-reality, of species. But the brief space remaining will permit scarce a reference to them. Moreover, single instances in biological fields can never prove general laws; they can, at most, illustrate them and prepare our minds for wider proof.

Let us look for a moment, however, at the group of little animals known as Hydra. Linnæus, with his long spoon, swallowed the whole genus at a gulp. He knew there were differences, as his description shows, but he called all by the one binomial, *Hydra polypus*. Soon, however, zoologists became convinced that Linnæus had been eating too fast. There were more species than one. But how many? Even yet unanimity has not been reached. Does this constitute an argument for the unreality or for the conventionality of species? In truth it does not. The genus Hydra has never been fully investigated. Interminable discussions of the undecipherable problems of priority have not been lacking; some good observations, and, much more to the point, some good culture experiments have been made. But year-long, controlled and pedigreed cultures are required, cultures successfully carried through sexual as well as asexual phases. Had these been carried out, as I trust they have been by the writer, the truth of the conclusion would have been amply demonstrated, that we have within the genus Hydra (whether or not we shall ever be able to name them) a number of highly autonomous aggregates of individuals, separated, the one from the other, by a large number of minute but highly constant differences. These groups are such as are commonly and appropriately called species, despite the fact that the ordinary student with the collecting bottle may be unable to distinguish them. To deny them reality or treat their systematic segregation as a matter of convention only is as inappropriate, because as untrue to the facts, as to deny the reality of any and all distinctions in nature.

Certain of these differential characters are of special

interest in connection with the problem of the separateness of species. Thus two of these groups that outwardly resemble each other the most, and whose distinctness is still doubted by some eminent zoologists, prove, under examination with modern technique, to be possessed of extraordinary histological differences. Hardly may we find in the whole mammalian series corresponding types of cells showing so fundamental differences in structure as are shown by the cnidoblasts of the two species which (since we must choose among the questioned specific titles) are probably to be designated as *Hydra fusca* and *H. diœcia*. Species, therefore, which Linnæus could not distinguish and which it may be hardly possible for the ordinary student to distinguish with the care commonly devoted to such subjects, may yet be separated by differences which seldom obtain between much more remotely related types.

Did space permit, I might also illustrate from this genus of organisms the proposition that the integrity, and hence the reality, of species is not destroyed by the fact that certain individuals of one may be transformed into members of another. I will but refer to the fact that it is possible, though extremely difficult, to transform *H. viridis* into another, a white Hydra (*H. fusca*), differing from it in practically every specific character. I do not refer to the mere bleaching of the green species. This, up to a certain point, is easy, but carries with it no significant morphological changes. The transformation which I have effected (in both directions) does carry with it such changes, and once produced they are extremely permanent through an indefinite number of generations and in spite of many environmental changes.

Of course we may, if we will, degrade these types from specific to varietal rank, although they probably deserve the specific distinction. But the point of emphasis is the relative autonomy of the two groups. I have never been able to even find them in the same habitat. Interbreeding is precluded by their sharply separated periods (fall and spring respectively) of sexual development. Species,

then, may be sharply demarcated despite of the possibility of reciprocal derivation.

Lastly I had wished to defend the seeming paradox that species may be not only real, but all but absolutely stable despite of the widest variability. This is not a contradiction in terms. The stability of a species depends upon its refusal to vary in certain given directions, *i. e.*, away from its specific characters, or, secondly, upon the non-transmissibility of such variations when once produced. The variability of a species, however pronounced, may mean only the production of non-specific characters or the production of characters of whatsoever order which are not repeated in the offspring.

Thus it proved to be with the species of salamander—*Amblystoma tigrinum*—upon which I spent several years of almost continuous experimentation. Variability and instability of species, when I began my work, for me were synonyms; when I concluded they had lost almost all relation in meaning. The astounding variation of this species was in the main but a somatic by-play in response to environing forces. However, wholly against first impressions, it turned out that this somatic variation, despite its variety and extent, yet had its marked limitations. How I did strive to make *Amblystoma punctatum* out of *A. tigrinum*—such a little thing, too—just to make a leopard salamander out of a tiger salamander. I did not even try it until my third season's experimenting. It was really too insignificant a task. Had I not observed nature working much greater changes?—and, by imitating her methods in experiment, had I not gained the key to her processes? Had I not passed the bounds of specific and even generic characters? Indeed, certain wise ones had nodded gravely, and suggested no less than family rank for the best of my handiwork. Just to make *A. punctatum* out of *A. tigrinum!* Besides I had the thing three quarters done already, time and again, as a by-product of my other work. At last I concluded, however, to make a few bona fide *A. punctatum* just for the fun, and to plague certain species people. And for season

after season I plagued myself at the rate of sixteen hours per day to accomplish this and other kindred things all relating to the stability or instability of this one species. And how much I accomplished, and yet how absolutely little. I made the characters all right, at least of the adult; unless possibly the special distribution of a few skin pores about the head eluded me. Last of all I even segregated the palatine teeth into groups and dragged them well back toward the throat in true punctatum style. It was easy, given time and the knowledge how. Though alas, while I was corralling this chief character, the whole herd of lesser ones which I had previously rounded up were absolutely certain to escape me.

In short, my seeming success was abject failure. Characters, but never in perfect combination; and then, not a trace of tendency toward transmission. I found no mordant of conditions penetrating enough to bring germ cells into the slightest harmony with my special somatic policies.

Species unreal! It may be that they are in some ghostly sense toward which my imagination has not wandered. It may be that many alleged species are unreal enough. But the majority of those with which I have dealt, although chosen for the very reason of their seeming or possible unreality, so to speak, have yet left upon my mind the impression of *almost* indissoluble entities.

An exaggerated impression it may be. Had I been collecting facts about geographical races, for example, I might have verged toward other conclusions. But such study, if it makes for a seeming fluidity of nature, is confessedly but tentative and superficial, and its facts about species are but a part of the facts. Does Mendelianism, for instance, with its unit characters and its mathematics of heredity, make for the unreality of species? Do modern experimentalists claim to be dealing with species as concepts only?

This leads to a last word. Is it of any importance how we think of species? May we, equally well, think of species as conveniently segregated groups of more or less

similar objects, associated for convenience sake with a single appellation; or as correlated, genetically unified groups, as segregated portions of reality (convenient or inconvenient for our intelligence) which nature somehow sets apart, regardless of whether we know and name them or not? To the writer it seems a matter of the first importance. If organic nature is so fluid that our distinctions are conventional only, if specific names are but handy helps by which we point out this or that sizeable mass of organic territory, then must our whole attitude be altered accordingly. It is no wonder that those who hold this view are satisfied with nothing short of a general knowledge of a whole fauna or flora. But if species are downright realities (as science counts reality), subtle, illusive realities, perhaps, still less than half understood, yet existent, demanding ever more exact definition and deeper explanation, then their knowledge becomes a new and better thing, and the impetus they offer to investigation is wholly changed. Then must we recognize the right to modify Linnæan species whenever they disagree with reality, however much we respect Linnæan authority.

The whole spirit of modern biological research seems to the writer to demand the conception of species as realities,—not all alike, in their reality, of course. Linnæan species, elementary species, physiological species, ontogenetic, phylogenetic species,—these and more may well prove to be essentially unique phases of nature's reality. But does not the thought of the investigator that steadies itself by these conceptions of species as realities fully justify itself by results?

And if there are other reasons for the assertion of the unreality of species, over and above the return to that child-like thought which sees reality only in the obvious units of perception, over and above a carelessly exaggerated idea of variation as obliterating all but conventional distinctions, what, we ask, are they?

SHORTER ARTICLES AND DISCUSSION

A LIGHT-WEIGHT, PORTABLE OUTFIT FOR THE STUDY AND TRANSPORTATION OF ANTS

1. *Nests.*—For some time I have been observing ants in artificial nests. I have used Fielde (1900–1904) nests ten inches long and six inches wide, a size which needs cleaning less often than the sizes used by Miss Fielde, and gives the ants, especially species of large stature, more freedom. Though these nests are in most respects satisfactory they have proved, when of this size, to be too heavy to be easily carried about on a journey. In order, therefore, to diminish the weight, nests of the same general plan as Fielde nests were made of aluminum instead of glass. Necessarily, however, the construction was quite different from the prototype. From a flat sheet of light-weight aluminum (0.28 mm. thick) was cut a piece of the form shown in Fig. 1. Aluminum of this thickness can easily be cut with an ordinary pair of sheers. The lines *c*, *d*, *g*, *h*, and *e*, *f*, *i*, *j*, were ruled on the aluminum with a lead pencil; at each of these lines the metal was bent at right angles by a tinsmith. Thus *k*, *l*, *m*, *n*, became the vertical sides of a shallow tray one half inch deep, while *o*, *p*, *q*, *r* became a practically continuous overhang projecting horizontally inward one half inch as a marginal part of the tray. The parts of *o*, *p*, *q* and *r*, which overlapped each other at the corners of the tray, were firmly fastened together by McGills' fasterners.[1] The tray, or nest was divided into two approximately equal chambers, *A* and *B*, by a partition five inches long. This was made of a strip of aluminum an inch and a half wide, bent, as shown in Fig. 1 (enclosed in chamber *A*). The base (*t*) was attached to the floor of the tray by means of three McGills' fasteners, one at each end and one in the middle (*s*, Fig. 1), so that *u* served as an upright between chambers *A* and *B*, while *v*

[1] A much better joint would be produced by a method of soldering aluminum; but when the first trays were made I was not aware that such a method was known. More recently it was learned through Professor A. G. Webster, of Clark University, Worcester, Mass., that a technician in his department had invented a method of soldering aluminum, and Professor Webster has kindly had soldered for me some of my trays.

formed an overhang over one of the chambers, and, together with *o*, *p*, *q* and *r*, served to support the glass roof-panes, one covering chamber *A*, the other chamber *B*. *v* was made half an inch longer at each end than *t* and *u*, the projecting ends resting on *o* and *p* to which they were fastened, thus giving the tray additional rigidity. As in the Fielde nests, the necessary ventilation and tightness of roof were secured by using strips of Turkish toweling, which were glued to the upper surfaces of *o*, *p*, *q*, *r* and *v*. All cracks in the corners and around the partition were stopped with putty. In one chamber a wet sponge was kept, and in the other food. Either chamber, or both, could be darkened by pasteboard covers placed on top of the roof-panes.

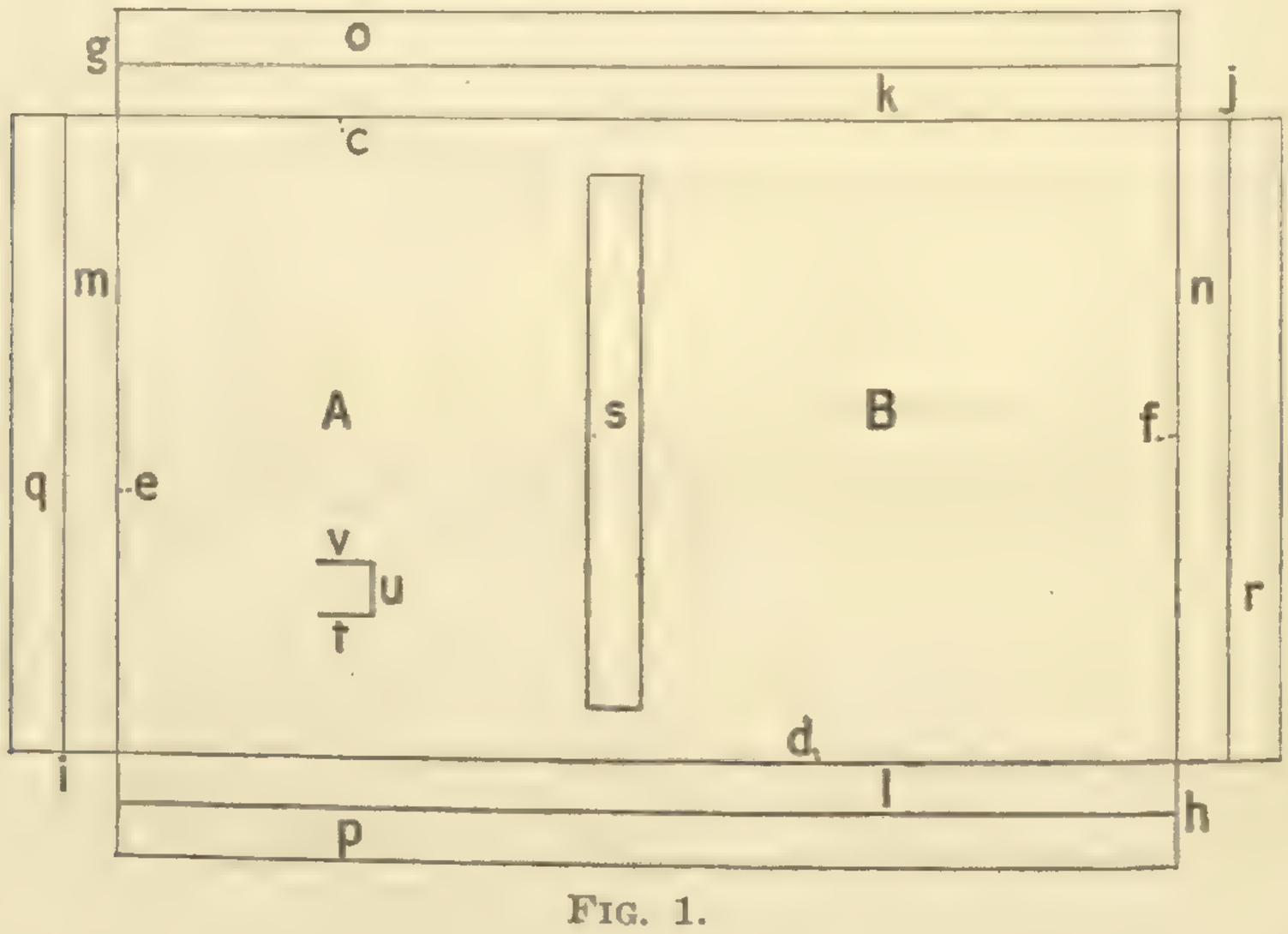


FIG. 1.

2. *Traveling Case.*—In order still further to diminish the weight of the outfit, and render it more convenient in traveling, certain modifications were made in the Fielde (1904, p. 28) traveling case. For part of the plan and all the construction I am indebted to my mother. The case (Fig. 3) was made as follows: The floor, roof and ends were made of wood three eighths inch thick, each composed of a pair of strips two inches wide, placed parallel to each other and two inches apart. Four strips of heavy tin, about six inches broad and as long as the width of the floor (about six inches) were bent at right angles, like "angle irons," to form the corners of the case where the ends met floor and roof. The strips were nailed securely to the tins, leaving the desired space of two inches between the strips of each pair. The case was twenty-one and a half inches long, six

and a half inches high and six inches from front to back, inside measurements, and it was divided into two chambers of equal size by a vertical partition. The back and front were made of book-binder's board, the back having a few large circular holes to allow for ventilation, and the front serving as a door. The entire case was covered with woolen cloth, which was carried over and nailed to the front edges of the case at top and sides, thus forming a cloth-covered jam for the door to shut against. The cloth covering at the bottom of the door served as a hinge.

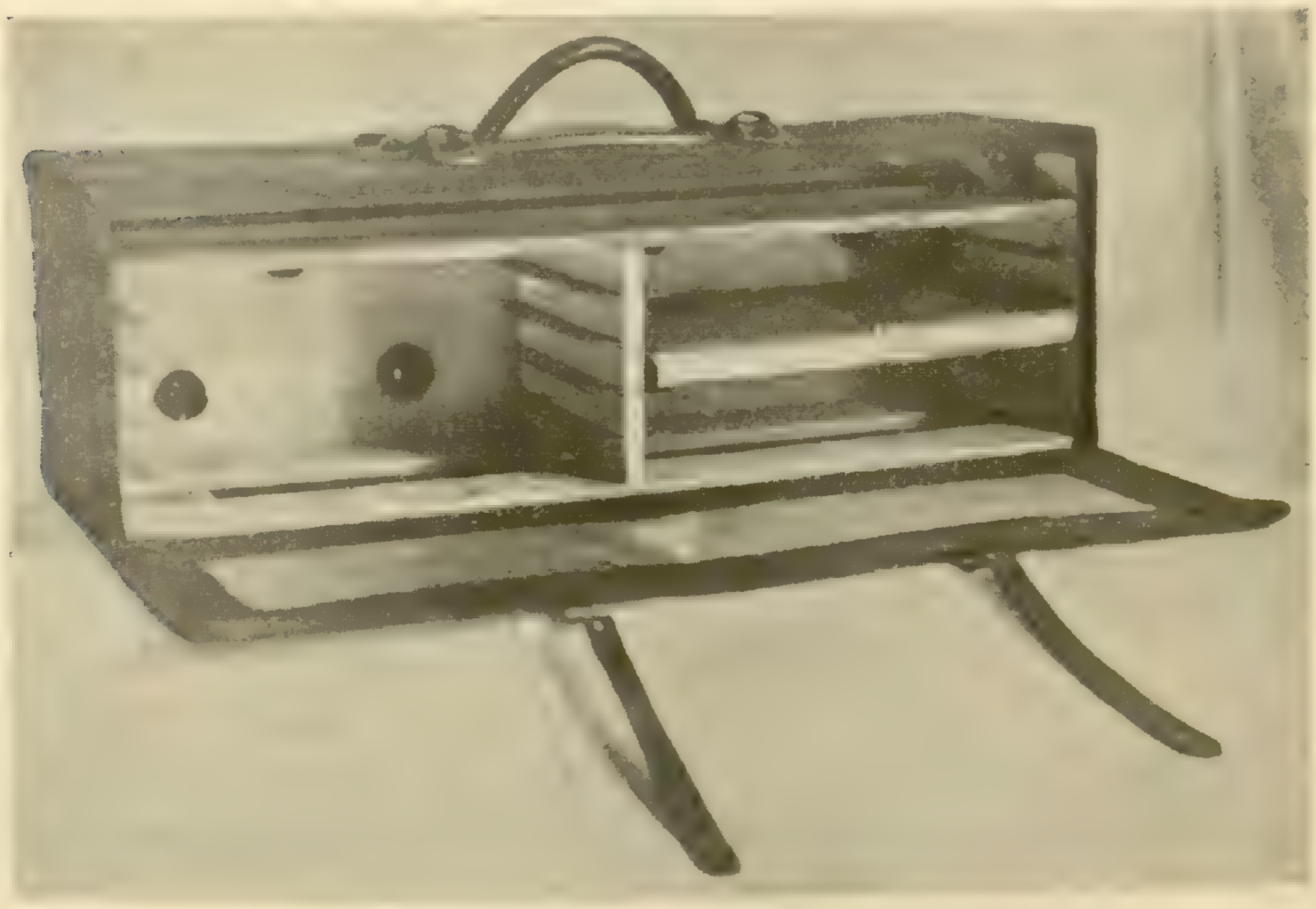


FIG. 2.

The door when closed was fastened by a brass ring which fitted over a screw in the front edge of the top of the case. The trays were supported on ledges made of strips of thick tin bent at right angles and screwed to the end walls of the chambers at suitable heights, as seen in Fig. 2, which shows one tray resting on its ledges and covered with its pasteboard mats. The corners of the tin ledges were rounded; to prevent the screw-heads from wearing the edges of the trays as the latter were inserted and withdrawn, the vertical part of the ledges and their screws were covered with strips of thick paper, glued to the walls between the ledges.

This case was designed to accommodate twelve nests, but since two of my trays were not of the standard size adopted for the rest, I provided for their accommodation by putting in a false

roof, cutting off the space for the two upper trays, and omitting the partition from this space. When packed with nests of the Fielde type the whole outfit weighed about twenty-six pounds; but when packed with my aluminum nests, only about half as much, the weight of the case alone being about six pounds.

A strong leather shawl-strap, with stout handle, was used in carrying the case.

PAPERS CITED

Fielde, Adele M., "Portable Ant-nests," *Biol. Bull.*, Vol. II, No. 2, 1900, pp. 81–85, 3 figs.

Fielde, Adele M., "Portable Ant-nests," *Biol. Bull.*, Vol. VII, No. 4, 1904. pp. 215–222, figs. 1–3.

EDITH N. BUCKINGHAM.

BOSTON, MASS.

COMPARISON OF CÆNOLESTES WITH POLYPROTODONTA AND DIPROTODONTA

Cænolestes has been described by Mr. Oldfield Thomas (1895) who placed it in the family Epanorthidæ of the suborder Diprotodonta, which includes several fossil forms described by Ameghino. Sinclair, however, in the "Report of the Princeton Patagonian Expedition" (1901–6) gives the name Cænolestidæ to these small Santa Cruz Diprotodonts, from the genus Cænolestes, which, although a modern form, is more primitive than any of these fossils in regard to the diprotodont character of the teeth.

In view of the phyletic interest attaching to this form, as perhaps the starting point for the evolution of diprotodont tooth structure, it was considered advisable to make more completely detailed drawings of the skull than had before been done, in respect principally to sutures and foramina, and to compare skull and other characters with types of Polyprotodonta and Diprotodonta.

The skull from which the accompanying drawings were made is the specimen which Sinclair figured in his report, loaned to me through the courtesy of Dr. J. A. Allen, from the collection of the American Museum of Natural History. I am indebted also to Mr. W. K. Gregory, of the museum, for many helpful suggestions during the course of the work.

Among the general marsupial characters of the skull of Cænolestes may be mentioned the following: absence of pituitary

fossa and clinoid process, terminal nares, nasals broad posteriorly, malar forming wall of glenoid fossa, premaxillæ not touching frontals; on the ventral surface—palatal vacuities and palatal ridge, small lamellar pterygoids, alisphenoid bulla, and annular tympanic.

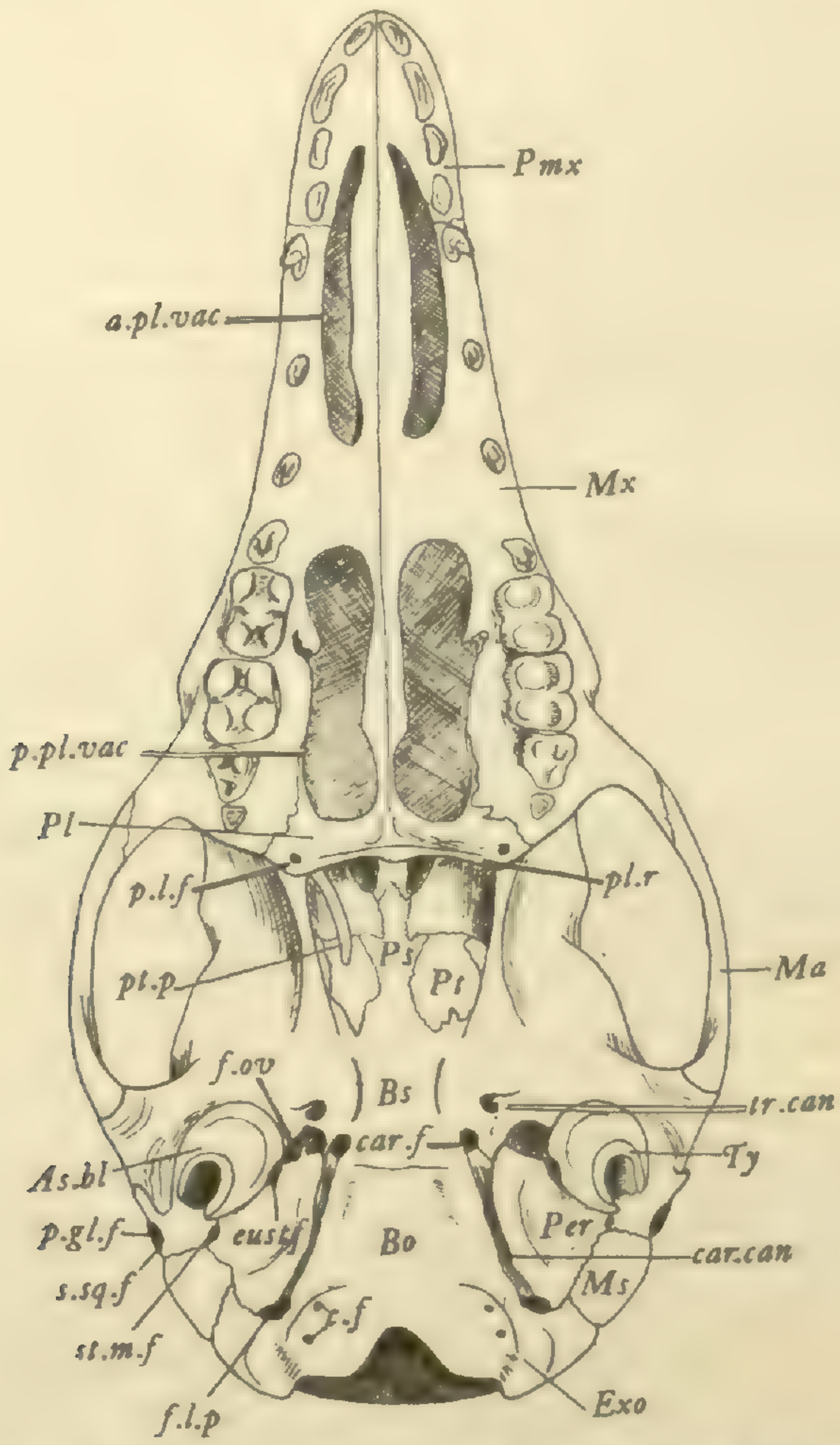


FIG. 1. Palatal aspect of cranium of *Cænolestes obscurus*, × 3. *As.bl*, alisphenoid bulla; *a.pl.vac*, anterior palatine vacuity; *Bo*, basioccipital; *Bs*, basisphenoid; *c.f*, condylar foramina; *car.can*, carotid canal; *car.f*, carotid foramen; *eust.f*, Eustachian opening; *Exo*, exoccipital; *f.ov*, foramen ovale; *f.l.p*, foramen lacerum posterius; *Ma*, malar; *Ms*, mastoid; *Mx*, maxilla; *Per*, periotic; *p.gl.f*, post-glenoid foramen; *Pl*, palatine; *p.l.f*, postero-lateral foramen; *pl.r*, palatal ridge; *p.pl.vac*, posterior palatine vacuity; *Ps*, presphenoid; *Pt*, pterygoid; *pt.p*, pterygoid process of palatine; *Pmx*, premaxilla; *s.sq.f*, subsquamosal foramen; *st.m.f*, stylomastoid foramen; *tr.can*, transverse canal; *Ty*, tympanic.

Marsupial characters in the foramina are seen in the following: foramen lacerum anterius confluent with optic (sphenorbital foramen); presence of postero-lateral palatine foramina, lachrymal duct on anterior margin of orbit, transverse canal, carotid foramen perforating basisphenoid, double condylar fora-

mina, subsquamosal foramen. In identifying foramina in the squamosal I have followed the descriptions given by Cope.

Two characters more or less peculiar to Cænolestes are, as mentioned by Thomas: pterygoid processes of palatine long, slender and delicate; ant-orbital vacuity between nasals and maxillæ, found elsewhere only in ruminants.

Polyprotodont Characters.

1. Dental formula like that of the Dasyurid genera Thylacinus, Phascologale, namely:

$$i\ \tfrac{4}{3}\ c\ \tfrac{1}{1}\ pm\ \tfrac{3}{3}\ m\ \tfrac{4}{3};$$

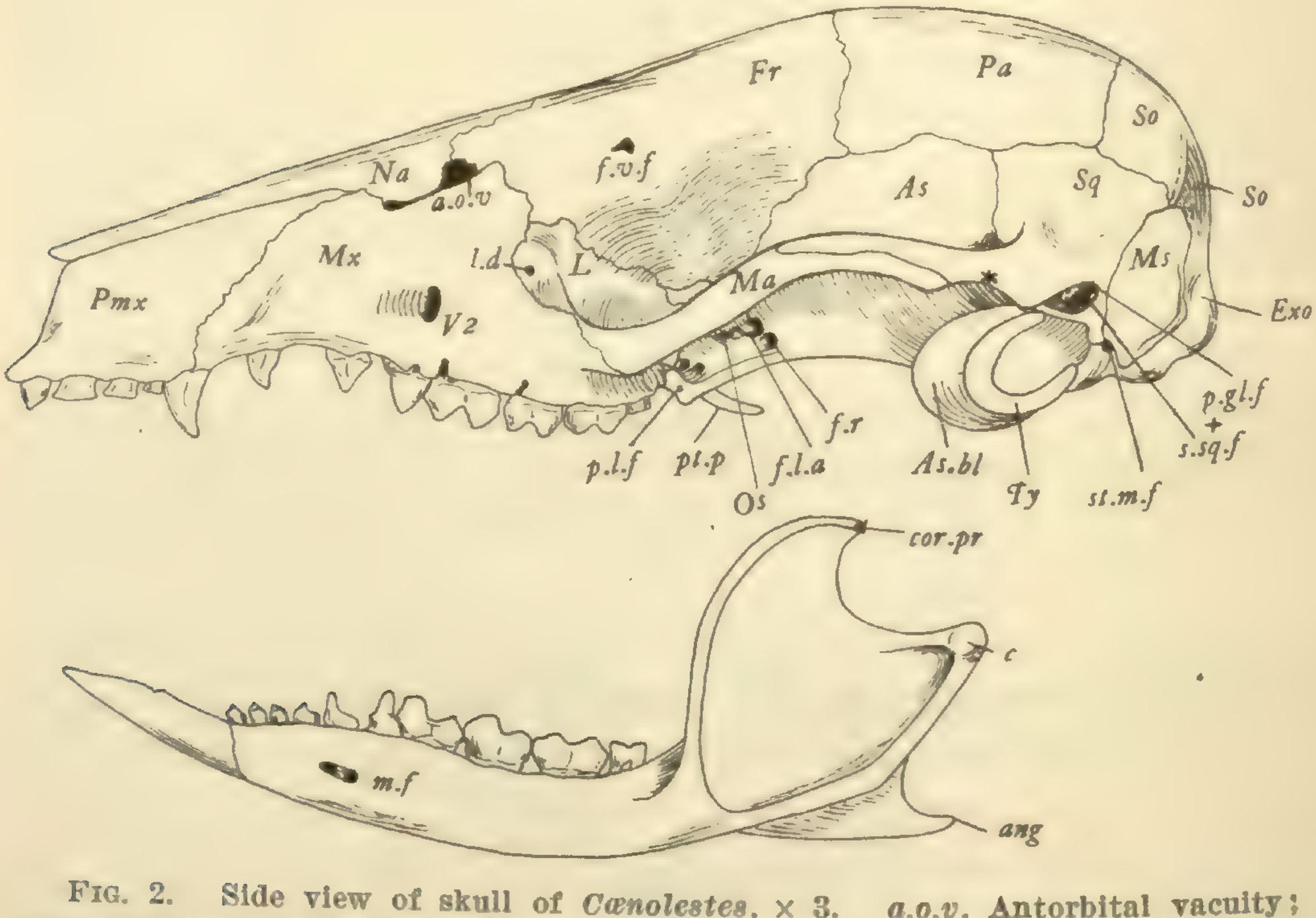


FIG. 2. Side view of skull of *Cænolestes*, × 3. *a.o.v*, Antorbital vacuity; *ang*, angle; *As*, alisphenoid; *As.bl*, alisphenoid bulla; *c*, condyle; *cor.pr*, coronoid process; *Exo*, exoccipital; *f.l.a*, sphenorbital foramen; *f.r*, foramen rotundum; *f.v.f*, venous foramen in frontal; *Fr*, frontal; *L*, lachrymal; *l.d*, lachrymal duct; *m.f*, mental foramen; *Ma*, malar; *Ms*. mastoid; *Mx*, maxilla; *Na*, nasal; *Os*, orbitosphenoid; *p.gl.f*, post glenoid foramen; *p.l.f*, posterolateral foramen; *Pa*, parietal; *Pmx*, premaxilla; *pt.p*, pterygoid process of palatine; *s.sq.f*, subsquamosal foramen; *So*, supra-occipital; *Sq*, squamosal; *st.m.f*, stylomastoid foramen; *Ty* tympanic; V^2, infra-orbital foramen. The * indicates the part of the cranium with which the condyle of the mandible articulates.

in this family the incisors are numerous, small, subequal, canines larger than incisors. This agrees with the condition in the upper jaw of Cænolestes.

2. Close resemblance in external form to Phascologale—rat-like or opossum-like in form (Thomas).

3. Resemblance to Dasyurus skull, (*a*) in general shape, (*b*)

pterygoid processes of palatine slender and delicate (in the specimen figured the process is missing from the left side), (*c*) alisphenoid bullæ similar in general form.

4. Marked resemblance to Antechinomys and Sminthopsis skulls in size, shape and delicate character of the bones; absence of strong crests or ridges.

5. Palate long and narrow, similar to characteristic Polyprotodont form, with long and narrow palatal vacuities.

6. Lower jaw very similar to Dasyurus, Phascologale, and especially to Antechinomys and Sminthopsis in inflection of angle, and proportionate size of angle, condyle and coronoid.

7. Rudimentary pouch (Thomas, after Tomes), as in Phascologale and Marmosa.

8. Fore and hind limbs about equal.

9. Pes non-syndactyl as in Dasyures and opossums.

10. Foot plantigrade—resembles Phascologale in number and position of pads, and short clawless hallux (Thomas).

Diprotodont Characters (Thomas, Sinclair).

1. Condition of teeth—(*a*) one large lower incisor, cutting, forward projecting, (*b*) other incisors and canine in lower jaw vestigial as in Epanorthidæ, (*c*) anterior premolars small, showing tendency toward condition seen in Phalangers, where they are vestigial.

2. Pattern of teeth—molars like Phalanger molars rather than the Polyprotodont type. In Petauroides and Trichosurus there are four cusps on incipient ridges; in Cænolestes the ridges have increased in extent to form a lophodont type.

Conclusion

Sinclair concluded that Cænolestes is very like the primitive Phalangers, and the two families are probably related, not convergent; that, while the fossil Cænolestidæ are too specialized in tooth structure to be the direct ancestors of the Phalangers, yet there is probably a common ancestry. Later, he gave weight to the possibility of convergence to account for the resemblance in tooth structure (p. 443). This latter view would seem to be more in accord with the facts known about Cænolestes, for excepting tooth structure, there appears to be no other important character which links it with the Diprotodonts and there are several, as given above, which link it with the Polyprotodonts.

While there is undeniably a series of forms connecting Cænolestes with the Diprotodonts in tooth structure, yet Cænolestes itself is so generalized in this respect that we may perhaps in the absence of other corroborating characters, question its inclusion within this group. Possibly it may be found to be an offshoot from the Polyprotodonts, as it appears structurally to be more generalized than any Diprotodont, and therefore it might well occupy a separate suborder, as Thomas suggested—the Paucituberculata of Ameghino.

PAULINE H. DEDERER.

COLUMBIA UNIVERSITY,
May 26, 1909.

LITERATURE

Cope, E. D. Foramina Perforating the Squamosal in Mammals. *Proc. Am. Phil. Soc.*, 1880.

Osborn, H. F. Evolution of Mammalian Molar Teeth. 1907.

Sinclair. Report of the Princeton Patagonian Expedition, 1896–1899. 1901–1906.

Thomas, O. On Cænolestes, a still Existing Survivor of the Epanorthidæ of Ameghino. *Proc. Zool. Soc.*, 1905, p. 870.

NOTES AND LITERATURE

COMPARATIVE PSYCHOLOGY

Bohn's "The Birth of Intelligence." [1]—The good critic, says Anatole France, is he who recounts the adventures of his soul among masterpieces. If the reviewer recounts his adventures with Dr. Bohn's fascinating book, he can perhaps give a better idea of it than in any other way. Dr. Bohn has for years been engaged in a study of the behavior of the animals of the seashore, as influenced by the conditions under which they live. His published papers set forth that the behavior of these animals—the worms, crabs, snails, sea anemones and the like—is wonderfully dependent on the past influences they have undergone: the changes of tides, of day and night, and the like, leave their records on the animals, so that after removal from these agents, the creatures still show the habits formed under their influence. Thus the behavior of these creatures is not fixed and final, but surprisingly modifiable. Such complete and overwhelming confirmation of the results and views that had been independently expressed by the present reviewer and going even beyond what he had anticipated, could not be received by him otherwise than with enthusiasm: he recommended the work to his friends and wrote a laudatory review;[2] as Bohn in the present volume notes with satisfaction, his work "surprised the Americans" (p. 71). But the reviewer's enthusiasm was met in some quarters by skepticism and criticism; it was pointed out that Bohn's results are largely given *en masse*, as it were, and with a striking lack of that precision of detail and of method which most of us have felt requisite for establishing scientific results; Yerkes in 1906 said, in a review of his papers, "They are not thoroughly satisfactory scientifically for they continually suggest questions, doubts and new problems."[3] The work was of precisely the kind, some urged, in which inaccuracy, carelessness or prejudice would enable one

[1] Bohn, Georges, "La Naissance de l'Intelligence," Paris, 1909.

[2] *Psychological Bulletin*, 5, 1908, pp. 180–183.

[3] *Journ. Comp. Neurol. and Psychol.*, 16, 1906, p. 238.

to reach results seeming to confirm whatever theory the author wished to establish.

It was, therefore, with special interest that the reviewer greeted the appearance of a general work by Bohn; on the one hand, it would naturally deal with phenomena that the reviewer is convinced are of special importance; on the other, it was hoped that the care and accuracy of presentation would be such as to remove all doubts as to the validity of Bohn's scientific results.

As to the first point, a general examination seemed to show one's best hopes gratified. The book might be called an amplification of the text—"The reactions of a living creature at a given moment depend not only on the present conditions, but on all the conditions of the past life—not only the life of the individual under consideration, but also that of its ancestors" (p. 259).[4] This is the spirit in which I have desired to see written a book on behavior.

The book is not put in the form of a connected account, but is rather a series of discussions of general topics and problems, illustrated by examples. Discussion of the work and views of other investigators occupies a large space; here the author paints in large, sweeping strokes, pronouncing as to good or ill with absolute confidence. This method makes lively reading, but it requires great and accurate knowledge of details and a most fair and judicious spirit to use it and remain scientific; without these qualities it is cheap, easy and misleading. The author's qualifications in these respects we shall inquire into later.

Many of the author's general principles and methods seem excellent; he attempts to distinguish the varied different factors in behavior; to establish definite meanings for terms long under doubt or controversy (so for example the term tropism); to search for objective factors everywhere; he recognizes fully the complexity and modifiability of behavior. The reviewer finds especially sympathetic the section on the uselessness of the idea of *instinct* as an analytic concept; the emphasis on the fact that all adaptation or "finality" is a problem, not a solution (p. 286); the idea of the "struggle against variation" (Ch. 15),

[4] This sentence is used by Bohn as a summing up of ideas expressed by Semon; it seems to me however to express the idea of this book, though here Bohn possibly might not agree.

and indeed many other matters. Even where he would disagree, the discussion is interesting and often valuable.

Little reading of the book is necessary to show, what has been evident from recent papers, that the author is a hero worshipper, and that at present the hero of his tale is (most deservedly in a book on the objective study of behavior) Jacques Loeb. Yerkes is given a place as a worthy follower of the master, while the present reviewer takes the rôle of the villain in the plot. It will be worth while to translate Bohn's characterization of three American investigators, as giving an example of his style of thought and expression. I quote from an article in the *Revue Scientifique* of May 16, 1908, which gives some picturesque features not taken into the book.

I have pronounced the name of Galileo; I can not resist the temptation to inscribe by the side of this name that of the biologist JACQUES LOEB.

Certainly since Galileo times have changed. No longer are revolutionary savants persecuted, at least not openly. There are free countries such as America for men such as Jacques Loeb. Beyond the Rocky Mountains, on the shores of the most beautiful bay in the world, at Berkeley, opposite San Francisco, are the laboratories whither the Californians have called the great biologist; it is in a scene truly fairy-like that Loeb works without ceasing and whence he sends forth the ideas which pass through the world to give a significance to biological researches.[5]

However, in America they continued to gather facts. And a savant of great worth, YERKES, completed without noise the work of Loeb[6] by searching out, with a spirit of method truly remarkable, how associations are formed in animals; his two memoirs on the acquisition of habits in the frog and the crayfish will remain classic and must serve as models to all those who attack the same questions. Yerkes has shown a quality that is rare among psychologists; that of not attempting to choose a personal attitude and to attach his name to a system; he has endeavored constantly to establish facts with all the rigor desirable and to give to them wise interpretations.

Suddenly[7] JENNINGS appeared on the scene; he presented a system;

[5] This passage is found also on page 42 of "La Naissance de l'Intelligence."

[6] The precise reference here seems to be to "the phenomena of association studied by Loeb in the lowest animals," words which he has employed a little before.

[7] The fact is of course that I had been publishing papers on this line of work for a number of years before Yerkes began; and that I suggested

that of trial and error, with disciples already numerous, he undertook a crusade against what he called the "orthodox theory of tropisms"; he cast trouble into the spirits, and certain ones could believe for an instant that the work of Loeb was about to crumble. It remained entire. The hurricane which had made such ravages in America made itself felt even in Europe, where it had little trouble to demolish the frail constructions of M. Nuel.[8]

The part sketched for the third actor in the plot is certainly an unworthy one, but there is after all something dramatic about figuring one's self, after Bohn, as a sort of demon that rides upon the storm, carrying trouble to the poor creatures of earth; so this, with the pleasure of seeing the ideas of the complexity and modifiability of behavior in lower organisms for which I have long worked, so completely triumphant in Bohn's book, must perforce be my consolation. It is the traditional fate of innovators to suffer condemnation that their work may prevail.

But there remains the second point to consider; in the book the author gives us a study not only of phenomena at the seashore, which we can not test for ourselves, but of the work and views of other investigators, which we can ourselves examine. Here is a test for the accuracy, thoroughness and conscientiousness of his work, for his mental grasp and his freedom from prejudice—a test for which we have above mentioned the need. Does he stand this test in a way to set at rest the doubts that have been expressed as to the trustworthiness of his scientific results in difficult fields?

For this test I naturally examined his presentation of my own work, since that is the matter with which I am best acquainted; furthermore I was of course curious to see why he presents me as one of the powers of darkness, while I have welcomed him as a support and ally. And here to my extreme disappointment I found things which I think may again "surprise the Americans" and every one else that has any ideals as to scientific accuracy. It would certainly be difficult for any author to the application of the idea of trial and error and criticized the theory of tropisms only after seven years of constant work, during which time I had published many papers on the subject. It is more dramatic to bring me in "tout à coup" and the shackles of chronology or other mere facts are not allowed by Dr. Bohn to interfere with effective presentation, as we shall see later.

[8] Le passé et l'avenir de la psychologie comparée," *Revue Scientifique* (50), 9, p. 624.

present a more thoroughly incorrect account of another's work, both as to material facts and as to general views and principles, than Bohn has given of my own. A citation of some typical examples will enable the reader to form an idea of the author's practise and ideals of accuracy.

Any one acquainted with my work on the reactions of lower organisms will recall that I found and set forth, with what seemed to many wearisome repetition, that the cause of reaction is in a large proportion of cases a *change* in external conditions, variation in concentration of chemicals, in degree of temperature, intensity of illumination, etc. Now, Bohn has likewise observed this (as had many previous workers), and he makes large use of it in explaining behavior; under the name of "sensibilité différentielle" it forms one of his three main factors in behavior. He is even inclined to lay claim to a certain originality in this.[9]

Amid the ruins [of other men's ideas] the reader, I hope, will see already some new constructions arising. Certain chapters, those consecrated to *vital rhythms* and to *sensibility to differences* figure for the first time in a book on comparative psychology (p. 3).

For this purpose it is convenient that he feels prepared to assert *that I had never recognized this as a cause of reaction!*

The idea of sensibility to differences has escaped Jennings.[10] In general, Jennings has not carried far enough the analysis of the movements of the lower organisms; as he has not taken account of the phenomena of sensibility to differences, he has been led to speak of "trial and error."[11]

Such statements appear again and again throughout the book, and form the basis for repeated condemnations of my work. It would be difficult to make statements more completely contrary to the facts. As this is the source of most of Bohn's mistakes in regard to my work, it is well to consider the matter in some detail.

No doubt is left as to what is meant by "sensibilité différentielle"; it is discussed in full with numerous examples; it is the

[9] Though he recognizes that Loeb had made use of the same idea.

[10] "La notion de sensibilité différentielle a échappé à Jennings," p. 179.

[11] "D'une façon générale, Jennings n'a pas poussé assez loin l'analyse des mouvements des organismes inférieurs; comme il n'a pas tenu compte des phénomènes de sensibilité différentielle, il a été amené à parler d'essais et erreurs," (p. 191).

same as Loeb's "Unterschiedsempfindlichkeit" and signifies reactions to changes in the environmental conditions. "Il s'agit, en effet, de réponses à des variations plus on moins brusques des diverses forces du milieu extérieur" (p. 167).

Consider in connection with the above statements from Bohn, the following: In the table of contents of my book on the "Behavior of the Lower Organisms" (1906), we find the caption Change of Conditions as a Cause of Reaction. Turning to the indicated chapter (XVII), as any one would naturally do who desired to form a conception of my results on this matter, we find that the second numbered paragraph begins:

> The most general cause of a reaction is a change in the conditions affecting the organism. This has been illustrated in detail in the descriptive portions of the present work (p. 293).

Practically the entire chapter is taken up with an analysis and discussion of variations in the environmental agents as causes of reaction. In the descriptive portions of the work the point is set forth most explicitly again and again. Taking the account of Paramecium as a type, we find the following:

> It is clear that the cause of reaction is the *change* from one solution or temperature to another (p. 51). The animal, having been subjected to certain conditions, becomes now subjected to others, and it *is the transition from one state to another that is the cause of reaction.* This is a fact of fundamental significance for understanding the behavior of lower organisms[12] (p. 52). But as its movements carry the animal from one region to another, the environmental conditions affecting it are of course changed, and some of these changes in condition act as stimuli, causing the animal to change its movements (p. 58). In the reactions to mechanical stimuli, chemicals, osmotic pressure, heat and cold, and powerful light, the avoiding reaction is caused by the transition from one external condition to another, by change in the intensity of action of some agent (p. 78). Examination has shown us that the cause for this reaction is some change in the conditions (p. 108).

For other organisms the point is likewise developed in detail and stated with equal explicitness. Thus, for Amœba: "The cause of a reaction—that is, of a change in movement—is in most cases some change in the environment" (p. 19); for Bacteria: "The reaction is caused as a rule by a change in the environment of the organism" (p. 37); for the reactions of Stentor to light: "all together, then, our experiments have

[12] The italics are in the original.

thus far shown that the cause of the avoiding reaction is the change from darkness to light'' (p. 131); for Euglena: ''It is clear that the reaction is due to the decrease in the intensity of light'' (p. 136); for reactions of infusoria in general to chemicals: ''The reaction is in each case caused by a change from one concentration to another'' (p. 123); for their reactions to light: ''To sum up, we find that the reactions to light occur in the infusoria in essentially the same way as do the reactions to most other stimuli. . . . The cause of reaction is a change in the intensity of light'' (p. 149). Pages could be filled with quotations from my book to the same effect.

In my earlier papers the matter is dealt with in an equally full and explicit way. My paper on ''Reactions to Light in Ciliates and Flagellates[13] is mainly devoted to showing in detail that the reactions are due to variations in the intensity of light. A section headed ''Nature of Agent causing the Reaction'' begins ''The primary and essential cause of reaction is a change of illumination'' (p. 65). My paper on ''The Behavior of Paramecium''[14] has a section headed Nature of Stimulation, in which we find the following:

> An examination of the facts shows that as a general rule the effective stimuli consist of some *change* in the conditions (p. 464).

These quotations are not isolated; they are mere typical sentences in an extended elaboration of the point set forth, and they could be multiplied almost indefinitely.

How then Bohn could make the statement that I had not taken account of this matter is inexplicable. But assuming that I was unacquainted with the fact that forms in reality the foundation of my presentation of the causes of reaction, the author of course cannot possibly understand my account of behavior; it is to him necessarily an edifice without foundations and must therefore crumble to earth. This is the source from which all of his misconceptions and (unintentional) misrepresentations of my work flow as naturally as water from a spring. The chief errors thus arising are the following.

1. He is necessarily utterly unable to understand my concept of ''trial and error.''

2. He is entirely prevented from grasping the nature of my criticisms of the tropism idea.

[13] Carnegie Institution, Publ. 16, 1904, pp. 29–71.

[14] *Journ. Comp. Neurol. Psychol.*, 14, 1904, pp. 441–510.

3. He is led to suppose that my account, being wrong in principle, must also be wrong in details, so that he attempts to correct details, by giving usually the same explanation that I had already given; or at times some other causal explanation that he devises, without experiment, to account for the facts; this often leads him into curious errors.

4. He is inevitably driven to suppose that I reject determinism in behavior.

5. He is naturally led (though here without real basis as it seems to me, save by additional error of the same sort) to attribute to me psychic, anthropomorphic and finalistic explanations in place of causal ones.

Let us look briefly at certain of these points.

1. My concept "trial and error" the author is forced by his mistake to suppose designed to take the place of an experimental analysis based on a real knowledge of the causes of reaction. His account of its origin is:

> As he has not taken into account the phenomena of sensibility to differences, he has been led to speak of trial and error (p. 191).

The fact is that the idea of trial and error was based precisely on reactions due to "sensibility to differences"; to changes in the conditions, and I have again and again stated that fact. For example:

> Just what is the nature of the stimulation which produces this reaction by "trial and error" in Paramecium? An examination of the facts shows that as a general rule the effective stimuli consist of some *change* in the conditions.[15]

The purpose of the concept was to bring under a unified point of view a complex of stimulations and reactions which had the interesting and important result of bringing the organism into conditions adapted to it, yet not including "anything differing in essential principle from such methods of action as we find in the inorganic world."[16] The concept is useful only in attacking the problem of how adaptation is brought about without the operation of "final causes." To speak of "trial and error" of course does not get rid of the necessity of finding a determining cause for every phase of the reaction, any more than to call a reaction "tropism" has this result. It has been pre-

[15] "The Behavior of Paramecium," *Journ. Comp. Neurol. and Psychol.*, 14, 1904, p. 464.

[16] "Behavior of the Lower Organisms," 1906, p. 343.

cisely my endeavor to show just how each phase was determined so as to show that "there is no evidence that a final aim is guiding the organism."[17] The application of the phrase "trial and error" to lower organisms arose as follows: The organisms react to changes in the conditions by movements of a peculiar character, which subject them to various environmental changes. Some of these changes cause them to react further, still further changing the conditions. Finally, as a rule, their continued movements bring them into conditions which do not cause them to react by further movements; since they do not react further they remain in these conditions. There is, as I have repeatedly attempted to show, evident experimental cause for every detail of this behavior.

We do not need any purpose or idea in the mind of the organism, or any "psychoid" or entelechy, to account for the change of behavior, for an adequate objective cause exists.[18]

But we need a name for such behavior; we need as it were to throw a net about it, gathering it together, so as to grasp its essential points, to the exclusion of unessential details. I have often characterized it as the selection of certain environmental conditions as a result of varied movements. For a briefer phrase, I found in common use for behavior in higher animals that is objectively similar, the expression "trial and error," so I employed this, specifying with the greatest care that it was only the similarity in objective features that I desired to bring out.[19] Later developments have shown that the designation was an unfortunate one, since readers not accustomed to distinguishing the phenomena on which a concept is based from other things that may be intermingled with it in particular cases are inclined to read into it in every case all that may occur in connection with it in any case; this seems to be Bohn's method of procedure. Other authors have found no difficulty in grasping the point involved; so Driesch in his recent volumes on the "Science and Philosophy of the Organism"; and Pillsbury in his paper on "Trial and Error as a Factor in Evolution."[20]

[17] *Ibid.*, p. 343.

[18] *Ibid.*, p. 342.

[19] See the note at the end of my paper on "Trial and Error," "Contr. to the Study of the Behavior of the Lower Organisms," 1904, p. 252; "The Behavior of Paramecium," *Journ. Comp. Neurol. and Psychol.*, 14, 1904, p. 461.

[20] *Pop. Sci. Monthly*, 1906, pp. 277–282.

where the concept is applied, in precisely the significance I gave it, to inanimate things. Objection to the phrase as liable to lead to misunderstanding among the uncritical I am glad to recognize as justified, so that I no longer employ it, but Bohn merely ranges himself among the uncritical.[21]

Bohn's inattention to my statements as to the cause of reaction of course leads him to suppose that whenever I speak of trial and error I mean that there is no experimental cause for the reactions; hence if he can show that there is experimental cause, this does away with the concept of trial and error! He therefore takes up a number of cases of reaction described by me (pp. 172–175, 187–195, etc.), shows, as I had done before, that they are due to changes in environmental conditions, and concludes that my exposition is wrong; that the application of the idea of trial and error is a mistake. His idea of trial and error is that it involves *chance*, in the sense of being undetermined.

By the analysis that I have made above, I have been led to reject many of the pretended trials and to show that the *chance* was most often only an illusion (p. 279).

In whose mind was the illusion? My own statement has been:

Everyone of these movements is, of course, as absolutely determined as the most orthodox tropism.[22]

Again, Bohn says: "Indeed, many of the sinuosities of the path followed by the lower animals can find an explanation in the combination of the tropisms and the phenomena of sensibility to differences" (p. 279), and in all seriousness he copies some of my figures and instructs me that the reactions shown are due to changes in the environmental conditions, just as I had shown before him. Some of the facts here are almost incredible; they throw a strange light on the author's accuracy and intelligent grasp. Thus, in the case of one of the figures copied from me (on p. 188), from which he draws on p. 191 the conclusion that I have "not taken into account the sensibility to differences,"

[21] It is a remarkable fact that in an earlier review of my book (*Bul. Inst. Gen. Psychologique*, 1906 (?), p. 282), Bohn understood correctly my usage of this phrase, as well as various other points that he now misunderstands. It would be most interesting to know the internal history of the change by which Bohn has been brought from a position of intelligent comprehension to one of blind misconstruction of my work. It is manifestly not due to further study of my work, since, as we have seen, he now shows extraordinary lack of acquaintance with the main points I made.

[22] *Journal of Experimental Zoology*, 3, 1906, p. 452.

in the very description of the figure, that I gave, both in my *Contributions* (p. 55) and my book (p. 139), *I stated repeatedly and in detail that the cause of the reaction was the change in intensity of the light.* I even pointed out on the figure just where this cause came into operation. I added this in the explanation of the figure (though given also in full in the text), in order that no one, however careless, could miss it; but Bohn has succeeded in doing so. In an account of the reactions of a ciliate infusorian that purports to correct my own, at the moment when the animal reverses its course the author says: "It is at this moment that I introduce the notion of sensibility to differences" (p. 193). This introduction having been made years before[23] and the acquaintance having been intimate ever since, the ceremony is hardly worthy of the solemnity with which the author invests it.

Bohn's inability to catch the idea of "trial and error" as I presented it is further due to two other points: (1) To speak merely of sensibility to differences seems to me quite insufficient for characterizing the reaction; the most important point is *what the organism does.* Different organisms do very different things and the same organism in different conditions reacts differently, under the same stimulus. What the organism does is the matter to which my attention has been primarily directed. Now, in those reactions that I called "trial and error" the organisms perform complex movements of such a character that they subject it to many different conditions. This was the basis for the use of the word *trial*, it meant this and nothing more. (2) Bohn is content to speak of "sensibility to differences," without analyzing the matter further. I carried the analysis much further, bringing out, not only the fact that the organisms react to some environmental changes and not to others, but that there is some system in this; that there is a relation between the changes to which the given organism reacts, and its own internal physiological processes; I tried to show that it reacts as a rule to changes that interfere with its physiological processes, in

[23] "The change in the solution at this point produces the characteristic reflex"; Jennings, 1900, *Amer. Journ. Physiol.*, 3, p. 399. "Many sorts of changes in the environment produce a certain characteristic reflex" etc.: Jennings, 1900, Woods Hole Biological Lectures for 1899, p. 104. "The direct cause of the reaction is a change in the nature of the surrounding medium": Jennings, 1901, *Amer. Journ. Physiol.*, 6, p. 35. See also quotations given on a previous page.

such a way that it leaves the region where these changes occur. It was here that I pointed out especially that for each step "an adequate objective cause exists." These relations, which Bohn neglects, are fundamental both for an understanding of the concept under discussion, and for any real understanding of behavior.

2. The same causes that prevent Bohn from understanding what I meant by "trial and error" equally prevent him from understanding my criticism of the tropism theory. He says:

> Jennings, from lack of having made the distinction between tropism and sensibility to differences, has been led to criticize, in an unjust manner, the tropisms of Loeb (p. 173). The notion of sensibility to differences has escaped Jennings; this investigator made the mistake of confounding it with that of tropisms, etc., etc. (p. 179).

Now, my reason for criticizing the application of the theory of tropisms was precisely because I *did* make the distinction Bohn speaks of. I dealt with a question of *fact*. The reactions of the organisms I studied had been commonly designated tropism (or taxis) and I used the same term until I had shown clearly what the nature of the reaction was. Then, being interested in the *facts* of behavior, I made an analysis showing that as a matter of fact the behavior did not consist of tropisms, that "the theory of tropisms is not of great service in helping us to understand the behavior of these lower organisms."[24] I can readily understand how it might be held that the theory *is* of service for certain reactions, but it is hardly worth while to attack my presentation on such mistaken ground as that I did not distinguish tropisms from reactions to variations in the environment. I have set forth in full my position on the tropisms in a recent paper,[25] so I may pass over it here. There is little in Bohn's impassioned defense of the tropisms that I could not assent to in principle; though I might object to the application to particular cases, and especially to the views which he attributes to me on the matter.

Points with which I could warmly agree are the following: He warns against "the deplorable results into which authors have been led by adopting the view according to which there would be tropisms everywhere" (p. 241). He says that "the activity of lower animals is composed of complex elements;

[24] "The Theory of Tropisms," Pub. Carn. Inst., 16, 1904, p. 105.

[25] "The Interpretation of the Behavior of the Lower Organisms," *Science*, May 1, 1908.

tropisms, phenomena of sensibility to differences, associative phenomena'' (p. 241) (he might have added others). ''It is very possible that the nervous system and the sense organs lend their help and facilitate the processes of which the tropisms are the consequence'' (p. 124); the tropisms are variable (p. 132); they are mixed with all sorts of other activities (p. 132). ''It is often said that the tropisms are *irresistible* movements, but this applies of course only to the case where the tropisms are of an intensity sufficient to overwhelm the animal; to annihilate its other motor manifestations'' (p. 132). A similar statement could of course be made for any cause of movement whatever. Bohn's definitions of the tropisms seem on the whole such as to command assent, though I reserve certain criticisms in detail, such as the strange bringing of the *will* into the definition of an objective phenomenon (p. 117, etc.).

As to the views attributed to me, Bohn says ''for him the tropisms would be the result of an apprenticeship; of long series of trials'' (p. 137). In this and similar passages the author follows his usual plan of making a positive statement without citation of his basis for it. I am not aware of ever having expressed any such view as is here attributed to me. On the contrary, I have said that the method of trial and error ''is in complete contrast'' with the tropisms,[26] while on the same page (and elsewhere) I have said that behavior of the stereotyped character of the tropisms occurs also.

3. As remarked above, Bohn assumes that it is necessary to correct my account in detail as well as in principle. His usual method, as we have seen, is to give the same explanation that I had already given. Either a feeling that nothing good could come out of my work, or his natural habit of mind, has led him in other cases into extreme carelessness of statement. One or two examples must suffice. On page 190 he says, in discussing my account of reactions to light:

> There is a factor of which Jennings has not taken account, it is the factor of *time*. *A certain time is necessary* for orienting itself.

Compare the following from Jennings:

> Thus the orientation is gradual and for a certain stretch after the light has begun to act the organism is not completely oriented. With a fairly strong light however, the period of time required for complete orientation is very slight.

[26] ''The Method of Trial and Error,'' Publ. Carn. Inst., 16, 1904, p. 50.

My entire analysis, properly understood, will be seen to largely depend on the fact that a certain time is required, and to be devoted to accounting for it. This analysis Bohn has evidently never looked into with care, since, as we have seen, he is not even aware that I attributed the reactions to variations in the intensity of light. It is well to give the devil his due; if one does it with care he may find he is not dealing with the devil at all!

Among the most remarkable feats of the author along this line is his attempt to recount and explain my description of the behavior of two amœbæ, one of which pursued and captured the other. The captor *a* after engulfing *b*, returns on its course, carrying the prey *b* (at 6, 11, 14 of Fig. 21 in my book; at 4 and 7 of Bohn's copy of the figure). Bohn says that the returning of the captor *a* is a mere recoil ("recul"), due to the *separating* of *b* from *a*; in place of *b* a glass rod would do just as well.

> The Amœba *a* quits with difficulty the contact with the solid body which one moves; when one breaks the contact suddenly the mechanical change which results from it for Amœba *a* determines the recoil of the latter.

In the description of the figure the author points out just where the "recoils" occur. Now the facts are, as I took pains to describe in my account, that this reversal of movement which Bohn calls the recoil (as at Bohn's *4*, *7*) takes place *not* when the prey escapes, but after the captor has enclosed it; having captured its prey the captor returns on its course. Bohn's explanation is then quite inadmissible. In copying part of my figure Bohn unfortunately omits precisely the portion that shows the larger amœba carrying the smaller after reversal of its course (at 6 of my figure).

4 and 5. I have given a sufficient number of illustrations of the author's accuracy and grasp of my work to make it easy to conceive the value of his accusations of indeterminism, of anthropomorphism; of such criticism as "Jennings has not carried far enough the analysis of the movements of the lower organisms." (This from a writer who does not so much as know that I attributed reactions to variations in the environmental conditions!)

[27] "Reactions to Light in Ciliates and Flagellates," Publ. Carn. Inst., 16, 1904, p. 59.

The attributions of indeterminism, anthropomorphism, etc., have their source in his mistaken statement that the idea of reactions to variations in environmental conditions had escaped me; in his book he places them on that basis. With the demonstration of his mistake on that point they fall to the ground. Let us put the matter clearly once for all. Either Bohn can or he can not cite passages from my work which justify his assertions and implications that I deny determinism and that I give anthropomorphic and non-objective explanations in place of causal ones. He has not as yet made, either in his book or his numberless papers, any attempt to give such citations. If he can do so, it would be worth while, that we may see on what basis he is proceeding. If he can not, to continue to make such statements is unscientific, for they are not verifiable.

Alas! then, we find that our author does not stand the test that we hoped might set at rest the doubts as to the accuracy and trustworthiness of his scientific results in difficult fields. I have not attempted to test the remainder of his account, but I fear that similar qualities might be found there. Has the author shown, in his account of the work above analyzed, accuracy and care of the same kind that he employs in reporting what happens in the infinitely more difficult field of nature? If not, why not? And if he has—How much are his scientific results worth?

From the literary standpoint the book is one that makes interesting reading, and many of the general ideas are worthy of attention. But such confusion, inaccuracy and misstatements of fact as we have pointed out above are almost or quite sufficient to remove it from the field of science.

H. S. JENNINGS.

MAMMALOGY

Osgood's Revision of the Mice of the Genus Peromyscus.—The genus Peromyscus is one of the most widely distributed and most numerously represented genera of North American mammals, its range including the whole continent from the Arctic barren-grounds to Costa Rica and Panama. It is, furthermore, one of the most interesting from the viewpoints of morphology and evolution, and also historically, in as much as it typifies and illustrates the progress of North American mammalogy. It includes, as at present restricted, only the small field mice

familiarly known as wood mice, deer mice, vesper mice (in allusion to their semi-nocturnal habits), or white-footed mice (from the fact that nearly all have white feet). They are at home in all sorts of environments, from moist woodlands to the open, semi-arid deserts, and vary in size from an animal smaller than the common house mouse to species nearly the size of a two thirds grown brown rat. The extremes of the group differ widely, not only in general size but in the size of the ears, the relative length of the tail, in coloration, and in dental and cranial characters. They are all subject, each after his kind, to a wide range of color variation, dependent upon age, season and abrasion of the pelage. They are also a plastic group, responding quickly to changes in the environment, so that quite diverse and geographically widely separated forms are often connected by an unbroken chain of intergrades, which renders the satisfactory allocation of closely allied forms extremely difficult, owing largely to the complications that have arisen from the bestowal of names upon what prove to have been intermediate forms. The naming of species and subspecies has been, in most instances, necessarily haphazard, since for a quarter of a century there has been no attempt to coordinate the work of the numerous describers who have raised the number of named forms from about a score in 1885 to fully 200 in 1908.

For several years Mr. Wilfred H. Osgood[1] has been at work upon a monographic revision of the genus, based upon a critical study of over 27,000 specimens, including the available material in all the principal collections, both private and public, in this country, supplemented by the examination of types and other important material in the museums of Europe. "This material," says the author, "includes all the types, both of valid forms and synonyms. In almost all cases in which no types exist, good series of topotypes, or specimens from near the type localities, have been available." The greater part of the specimens examined were collected by the Biological Survey, under the direction of Dr. C. Hart Merriam, with the special purpose of bringing together the material necessary for the proper monographic revision of the group. The results of Mr. Osgood's studies are

[1] "A Revision of the Mice of the American Genus Peromyscus." By Wilfred H. Osgood, Assistant, Biological Survey. Prepared under the direction of C. Hart Merriam, Chief of Biological Survey. North American Fauna, No. 28. Published April 17, 1909. 8vo, pp. 1–285, pl. i–viii, colored map, and 12 text figures (small distribution maps).

most welcome and will mark an era in the history of the genus, and for a long time to come will be the standard reference work for the group and the point of departure in future investigations.

The first member of the genus to receive a name was the common white-footed mouse of the northeastern United States, called by Kerr in 1792 *Mus agrarius americanus*, renamed *Mus sylvaticus noreboracensis* by Fischer in 1829, both authors regarding it as a variety only of a European species. By 1850 the number of named forms had increased to 9, to which were added 8 during the next decade, of which 13 were formally recognized by Baird in 1857. During the next twenty-five years only two or three new names were added to the list, but from 1885 on to date the number rapidly increased; "no fewer than 167 names for new or supposed new forms of Peromyscus," says Osgood, "have been proposed since 1885," to which 14 were added by him in the present paper, making a total of approximately 200 names to be dealt with in the consideration of the group. In the present revision 143 of these names are accepted as representing valid forms, of which 53 are given the rank of species and 90 are treated as subspecies. Of the 53 species, 23 are monotypic and 20 are polytypic, or include one or more subspecies, *P. maniculatus* including 35 forms, *P. leucopus* 12, and so on down to monotypic species. According to the author's own statement (p. 24): "The number of bona fide species scarcely exceeds forty, and of these some half dozen eventually may be reduced in rank."

In early days the white-footed mice, in common with all other mice, were referred to the Linnæan genus Mus. Later (1853–1874) they were referred to Waterhouse's untenable genus Hesperomys, a name replaced by Coues in 1874 by Vesperimus in a subgeneric sense for certain North American species formerly referred to Hesperomys, and later (1891) given full generic rank for the group of forms now placed under Peromyscus. It was soon discovered, however, that Vesperimus was antedated by Sitomys Fitzinger (1867), which name had hardly become current before it was found, in 1894, to be antedated by Peromyscus Gloger (1841), which bids fair to remain the accepted name for the genus. (This case is thus fully cited as an illustration of the vicissitudes of generic nomenclature in the attempt to secure permanency of names through the necessary application of the rule of priority.)

As already noted, while the group is a compact one, through the close interrelation of all the forms referred to it, the extremes of differentiation are widely diverse, but there are no trenchant lines of division, for, "if a single character becomes pronounced, it is merely an extreme development which may be traced back by stages to a widely different condition." Mr. Osgood, however, considers it desirable to recognize six divisions as subgenera, in order to indicate clearly the relationships of the diverse forms included in the genus. Two of them (Podomys and Ochrotomys) are here for the first time characterized; two others (Baiomys and Megadontomys) have been accorded by some authors the rank of genera, mainly as a matter of convenience in dealing with so large a group.

It would require too much space to go into details respecting Mr. Osgood's methods of dealing with the specially difficult cases, but the general outcome of his researches is of such general interest and has such a wide bearing that it seems desirable to give a few passages from his general introduction in his own words. Thus, under the heading "Variation" (p. 16), he says:

> Among western forms, variations of such an extremely local and sporadic nature often occur that one may almost believe them to have been produced in one or at most a very few generations. Such variations, of course, are slight, and doubtless produced immediately upon contact with certain conditions. Thus if the range of a given form includes a few square miles of lava beds, specimens from that area show an appreciably darker color than the normal form occupying the surrounding region. And whenever similar conditions are repeated elsewhere, even on a small scale, the same result seems to follow. Again, specimens from the bottom of a dark wooded canyon may be noticeably darker than those from an open hillside only a few hundred yards away. In the absence of absolute proof one can scarcely avoid the suspicion that if the progeny of paler individuals were transferred at an early age to the habitat of darker ones, they would, quite regardless of inherent tendencies, develop a darker color, or, similarly, a lighter color if the process were reversed.
>
> Local and geographic variations are great, so great indeed that, excepting a few species of very limited range, all the species have developed geographic peculiarities by means of which they have been subdivided into more or less numerous (geographic) races or subspecies. One species, *P. maniculatus*, which in its various forms ranges from sea to sea and from the Arctic Circle to the Isthmus of Tehuantepec, remains constant only where conditions are practically identical; hence it is represented by a definable subspecies in almost every faunal area which it enters. The readiness with which local variation is induced

and established appears also from the large number [22] of distinguishable insular forms. Much of the local variation, however, can not be considered subspecific. Certain forms, although preserving the same general characters throughout a definite range, nevertheless show slight and sometimes unique variations in nearly every local series from within the range. In these cases, where no two series of specimens from respective localities are exactly alike, and where no two can be associated except upon the basis of characters common to all, it is necessary to disregard slight variations and treat the entire association under one name.

Under "Intergradation" (p. 17) he continues:

Until recent years continuous and perfect intergradation was demonstrable only in relatively few cases. And even now, although proven beyond doubt in group after group, in many cases it is merely taken for granted. That intergradation exists even more widely than is generally supposed appears from the study of groups in which material is abundant. Of Peromyscus we have more complete series than of any other genus of American mammals; that is, not only are there more specimens, but many more localities are represented and the gaps in known distribution are usually few. Barriers impassable to many other mammals have little effect on these mice, for they range continuously, although not always without undergoing change, from sea level to great altitudes, and from the very humid to the very arid regions. Moreover, since usually they are so abundant and easily obtained, representatives are available from nearly every locality in North America ever visited by a mammal collector.[2] Within the range of one species (*maniculatus*) it is probable that a line, or several lines, could be drawn from Labrador to Alaska and thence to southern Mexico throughout which not a single square mile is not inhabited by some form of this species. They are wanting in the extreme north, but there is scarcely a corner south of the Arctic Circle in which they do not occur. With such wide and continuous distribution perfect intergradation must take place between related forms of different faunal areas, and with such complete collections this intergradation must be plainly evident in nearly all cases.

Classification becomes, then, as has been said,[3] like dividing the spectrum and depends largely upon the standards set, for, theoretically at least, the possibilities of subdivision are unlimited. It is not strange, therefore, that hundreds and even thousands of specimens are intergrades almost equally resembling two or more adjacent forms. Many

[2] American collectors of wide experience, in comparing notes, regard as worthy of remark the few occasions on which they have found themselves in localities where they "couldn't catch Peromyscus," and in such places, as a rule, they were also unable to catch anything else.

[3] Ridgway, "Birds North and Middle America," Pt. I. p. x, 1901.

of these intergrades for convenience may be referred with some degree of assurance to the form they most closely resemble, but many specimens fall so near the imaginary line between two or more subspecies that it is practically impossible to classify them other than as intergrades. A particularly troublesome class is one which approximates the color of one form and the cranial characters of another, thus reducing the question to one of relative importance of characters.

In view of the foregoing it is evident that taxonomic difficulties can easily arise, not only in this but in many other large groups of conspecific forms, through the unconscious, and hence unavoidable, bestowal of names upon intermediate and unrepresentative variants—upon connecting links between types that reach their full development at some more or less distant point from the locality which happened to be represented by the early describer's limited material. While his act may have been justifiable at the time from the circumstances of the case—absolute ignorance, due to lack of material then nonexistent in collections, of the range and variants of the group as a whole—it has resulted in difficulties of synonymy and procedure that must forever involve the subject, and introduce the element of personal equation into their settlement. As said by Osgood,

> The reviser is often confronted with three names representing steps in development, . . . one of the designated forms being intermediate between the other two. If, as often occurs, the recognition of only two forms seems necessary, and the intermediate has been named before either of the extremes, its name, having priority, must stand, and it beomes necessary to decide which of the names representing the extremes shall be considered a synonym. . . . A reviser in dealing with such names is compelled first to determine the number of recognizable forms without regard to names.

The type specimens are then referred, according to their resemblance, to the recognizable forms, and the names of the forms determined by the rule of priority.

Another difficulty is the temperamental, the viewpoints of different authors as to what degree of differentiation entitles forms to recognition. In the main Mr. Osgood has taken what appeals to the present writer as a judicial course, and has threaded his way with good judgment through the maze of difficulties inseparable from his subject. At all events he has methodized and correlated our present knowledge of the group, and clearly presented the relationships of the scores of minor forms that compose it. For the present at least it may be accepted and honored

as the last word, but of course not as the final adjustment, which must come slowly, as new material is gathered from the lesser known areas of the range of the genus, especially from the region south of the United States.

His paper is accompanied by a key to the species, and also by keys to the subspecies where such are required. A colored map shows the distribution of the species and subspecies of the *Peromyscus maniculatus* group, with indication of the intergrading areas between the recognized forms. The twelve text figures consist of small maps showing the range of all of the other species and subspecies. There are also tables giving the average and extreme external and cranial measurements of series of specimens of each form. Seven of the eight plates illustrate the skulls of some fifty or more species and subspecies (from photographs), while plate eight gives enlarged figures of the teeth and soles of the several subgenera.

It is to be regretted that the bibliographical references are restricted to the citation of synonyms, and thus fail to give clues to the work of previous authors, so essential to subsequent investigators in following up the history of a species or group, and hence of high importance in monographic treatises like the present. Aside from the convenience such references afford, they are important as a means of coordinating definitely, from the monographer's standpoint, the work of previous authors. Furthermore, in the lists of "specimens examined," only the localities and number of specimens from each are mentioned, the name of the collector and the collection where the specimens are located being omitted, thus giving no clue to the particular specimens to which the monographer refers. This, however, is obviously due to a faulty system of treatment rather than to the preference of the author, since the same method characterizes the long list of important monographs issued under the auspices of the Biological Survey. The addition of these essential items of information would considerably increase the amount of text, and for this reason have perhaps been omitted, since it is known that, for a long time at least, the restriction placed by the officials "higher up" in the Department of Agriculture on the technical publications of the Biological Survey were practically prohibitive of monographic papers exceeding a certain number of pages.

J. A. Allen.

American Museum of Natural History,
New York.

LÉO ERRERA

In Memoriam Léo Errera.—One can not ask for more loyal friends than those who have undertaken to keep alive the memory of the Belgian botanist Léo Errera, who died August 1, 1905, in his forty-seventh year. Botanists throughout the world have been favored with publications relating to the life of the lamented author and investigator, and volumes of his collected papers. The little volume, "Notice sur Léo Errera," by Leon Fredericq and Jean Massart tells pleasantly the story of his life and labors and recreations, and closes with a chronologically arranged bibliography of his writings, including nearly three hundred entries. His first paper appeared in 1874 when but sixteen years old, and this was followed a year later by two papers (one botanical), and from this time they appeared annually in increasing numbers, almost to the day of his death. In fact, ten papers were published posthumously by friends and colleagues who arranged or completed them for publication. A list of the "distinctions" bestowed upon him, includes his membership in various scientific societies, as well as the diplomas, medals, etc., which were awarded him.

Of the series of volumes planned to include a collection of his works under the general title of "Recueil d'Œuvres de Léo Errera" three are already published. The present arrangement includes six volumes. Volumes I. and II. are devoted wholly to Botany. The first contains papers on the Vegetation of the Environs of Nice, a review of Schuebler's "Pflanzenwelt Norwegens," the structure and modes of reproduction of flowers, heterostyly of primroses, a critique on systematic botany, suggestions as to certain neglected researches on bacteria and compass plants. The second volume contains papers on the respiration of plants. Latin names of plants, the scientific basis of agriculture, plant physiology, algæ, Darwinism, relation of plants to environment, the composition of plants, rays of sunlight. This list of subjects must serve to show the interest which these volumes must have for the botanist. Volume III. which is not yet published, will contain papers on general physiology; Volume IV., not yet published, will include philosophical papers, largely botanical; Volume V. is to be pedagogical and biographical. Volume VI, containing miscellaneous poetical and prose papers, has already appeared. It gives one another view of this versatile man.

CHARLES E. BESSEY.

Methods in Plant Histology

By CHARLES J. CHAMBERLAIN

Second edition, revised and much enlarged; 272 pages, with 88 illustrations, 8vo, cloth; net $2.25, postpaid $2.39

THE first complete manual to be published on the subject of botanical microtechnique. It contains detailed directions for collecting and preparing plant material for microscopic investigation, setting forth the advantages and disadvantages of the different methods.

"Will no doubt find a place in every well-regulated library, and will be found very useful by private students."— *Plant World.*

"It is an excellent book for the individual worker and for classes in colleges." — *Education.*

A Laboratory Guide in Bacteriology

By PAUL G. HEINEMANN

158 pages, interleaved, with 37 illustrations, 12mo, cloth; net $1.50, postpaid $1.61

A CLEAR and concise presentation of bacteriological technique, designed principally as a manual for the medical student, but highly useful also as a reference book for the biological teacher and investigator, as well as for practical workers in the fields of medicine and hygiene.

"The instruction given is clear and accurate, and the practical exercises are well selected." — *The Lancet* (London).

"A book such as this must facilitate very greatly the practical class work, for which it is most excellently adapted." — *American Journal of Medical Sciences.*

"The directions are clear and concise, and every stage is described so carefully that it is hard to see how the student can go astray. Physicians who are rusty in bacteriology cannot do better than buy this little book. The book is beautifully printed and bound." — *American Journal of Clinical Medicine.*

Animal Micrology:

Practical Exercises in Microscopical Methods

By MICHAEL F. GUYER

250 pages, 8vo, cloth; net $1.75, postpaid $1.88

THE title of this book will explain its scope. It is intended as a laboratory manual for textbook use. Its aim is to introduce the student to the technique of microscopic anatomy and embryology, emphasizing details of procedure rather than descriptions of reagents or apparatus. Sufficient account of the theoretical side of microscopy is given to enable the student to get satisfactory results from his microscope.

The directions are simple, explicit, and complete. — *American Journal of Clinical Medicine.*

The medical student will find it very useful as a guide to microscopic work. — *Journal of the American Medical Association.*

This is one of the cleanest works on microscopical technique we have ever seen, and is especially suitable for the beginner. It is full of points, tricks of technique not mentioned in other works, and is one that every student and physician should have. — *Medical Century.*

This valuable book is strong through its rigid exclusion of the trite and the conflicting. It is lucid and helpful, because a man long practiced in practical work has given what he believes the most expeditious and reliable method of obtaining a definite and comprehensive result. — *Medical Notes and Queries.*

A concise, eminently practical, and well-classified treatment. — *Science.*

The expositions of the methods recommended are admirably clear. — *Nature.*

One of the best and most practical works upon microscopic technique with which we are acquainted. — *American Naturalist.*

As a textbook it can hardly be improved. The research worker will find in this book just the information he frequently needs in preparing material with which he is not familiar. — *School Review.*

It does present in very clear form a judicious selection of methods, including an excellent untechnical account of the microscope and its optical principles, adequate for the undergraduate course in histology. — *Journal of Comparative Neurology and Psychology.*

ADDRESS DEPT. 62

Chicago **The University of Chicago Press** **New York**

The American Naturalist

A Monthly Journal, established in 1867, Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Organic Evolution and Heredity

CONTENTS OF THE APRIL NUMBER

Heredity of Hair Color in Man. GERTRUDE C. DAVENPORT and CHARLES C. DAVENPORT.

A Mechanism for Organic Correlation. Professor G. H. PARKER.

Recent Advances in the Study of Vascular Anatomy.
Vascular Anatomy and the Reproductive Structures. Professor JOHN M. COULTER.
The Progress of Plant Anatomy During the Last Decade. Professor EDWARD C. JEFFREY.

Shorter Articles and Correspondence: A Note on the Degree of Accuracy of the Biometric Constants, DR. RAYMOND PEARL. Pure Strains as Artifacts of Breeding. O. F. COOK.

Notes and Literature: *Heredity*—The Nature of "Unit" Characters, DR. W. J. SPILLMAN. *Environment*—DR. FRANK E. LUTZ. *Experimental Zoology*—Hybridology and Gynandromorphism, Professor T. H. MORGAN. *Echinodermata*—Red Sea Crinoids, DR. AUSTIN HOBART CLARK.

CONTENTS OF THE MAY NUMBER

The Categories of Variation. Professor S. J. HOLMES.

The General Entomological Ecology of the Indian Corn Plant. S. A. FORBES.

Notes and Literature: *Biometrics*—Some Recent Studies on Growth. DR. RAYMOND PEARL. *Experimental Zoology*—Cuénot on the Honey Bee, Professor T. H. MORGAN. *The Upholding of Darwin*—Poulton and Plate on Evolution, V. L. K.

CONTENTS OF THE JUNE NUMBER

Heredity and Variation in the Simplest Organisms. Professor H. S. JENNINGS.

The Color Sense of the Honey Bee — Is Conspicuousness an Advantage to Flowers? JOHN H. LOVELL.

Variation in the Number of Seeds per Pod in the Broom, Cytisus scoparius. Doctor J. ARTHUR HARRIS.

Present Problems in Plant Ecology:
The Trend of Ecological Philosophy. Professor HENRY C. COWLES.
The Present Problems of Physiological Plant Ecology. DR. BURTON LIVINGSTON.

Notes and Literature: Notes on Evolution, V. L. K. DeVries's Species and Varieties, DR. GEORGE H. SHULL. *Embryology* — On the Totipotence of the First Two Blastomeres of the Frog's Egg. DR. J. F. MCCLENDON.

CONTENTS OF THE JULY NUMBER

Selection Index Numbers and their Use in Breeding. DR. RAYMOND PEARL and FRANK M. SURFACE.

A Contribution to the Theory of Orthogenesis. DR. ALEXANDER G. RUTHVEN.

The "Presence and Absence" Hypothesis. Dr. GEORGE HARRISON SHULL.

Present Problems in Plant Ecology: Vegetation and Altitude. Professor CHARLES H. SHAW.

Shorter Articles and Correspondence: Pleistocene Swamp Deposits in Virginia. Dr. EDWARD W. BERRY.

Notes and Literature: *Heredity*—A Case of Non-Mendelian Heredity. DR. W. J. SPILLMAN.

CONTENTS OF THE AUGUST NUMBER

The New Flora of Krakatau. Professor DOUGLAS HOUGHTON CAMPBELL.

A Male Crayfish with Some Female Organs. Professor E. A. ANDREWS.

Present Problems in Plant Ecology:

Problems of Local Distribution on Arid Regions. Professor VOLNEY M. SPAULDING.

The Relation of the Climatic Factors to Vegetation. Professor EDGAR N. TRANSEAU.

Notes and Literature: Recent Experiments on the Inheritance of Coat Colors in Mice, Professor T. H. MORGAN. Some Experiments in Breeding Slugs. Professor T. D. A. COCKERELL.

CONTENTS OF SEPTEMBER NUMBER

On an Early Tertiary Land-connection between North and South America. Dr. R. F. SCHARF.

Notes on the Relations of the Molluscan Fauna of the Peruvian Zoological Province. Dr. WILLIAM HEALEY DALL.

Remarkable Development of Starfishes on the Northwest American Coast; Hybridism; Multiplicity of Rays; Teratology; Problems in Evolution; Geographical Distribution: Professor A. E. VERRILL.

Shorter Articles and Correspondence: Is there a Selective Elimination of Ovaries in the Fruiting of the Leguminosæ: Dr. R. HARRIS.

Notes and Literature: *Ichthyology*—Ichthyological Notes, President DAVID STARR JORDAN. *Parasitology*—Professor H. B. WARD. *Plant Cytology*—The Permanence of Chromosomes in Plant Cells, Dr. BRADLEY M. DAVIS.

Single Number 35 Cents **Yearly Subscription, $4.00**

The NATURALIST will be sent to new subscribers for four months for One Dollar

THE SCIENCE PRESS

Garrison, N. Y. **Sub-Station 84: NEW YORK** **Lancaster, Pa.**

VOL. XLIII, NO. 515 NOVEMBER, 1909

THE AMERICAN NATURALIST

A MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

CONTENTS

Page

I. The American Toad (Bufo lentiginosus americanus, LeConte). NEWTON MILLER. . 641

II. Notes on the Behavior of the Domestic Fowl. PHILIP B. HADLEY. . . 669

III. Vitality of Pine Seeds and the Delayed Opening of Cones. Professor W. C. COKER. 677

IV. The Affinities of the Echinoidea. AUSTIN HOBART CLARK. 682

V. The Early Breeding Habits of Amblystoma punctatum. ALBERT H. WRIGHT and ARTHUR A. ALLEN. 687

VI. Notes and Literature: *Marine Biology*—Papers from the Tortugas Laboratory, Professor WILLIAM E. RITTER. *Experimental Zoology* — Inheritance of Color in Pigeons, B. B. HORTON. 694

THE SCIENCE PRESS

LANCASTER, PA. GARRISON, N. Y.

NEW YORK: SUB-STATION 84

The American Naturalist

MSS intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS

Lancaster, Pa. Garrison, N. Y.

NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

Important New Scientific Books

PUBLISHED BY THE MACMILLAN COMPANY

Botany

The Origin of a Land Flora. A Theory based upon the facts of Alternation. By F. O. BOWER, Sc.D., F.R.S. With numerous illustrations.

Cloth, gilt top, xi+727 pp., illus., index, 8vo, $5.50 net.

NOTE.—A profound study in the morphology of the lowest forms of plants, with special reference to the development of their reproductive systems. The author endeavors to show that the present land flora has originated from an aquatic ancestor, and traces the methods of specialization to the land habit, and the establishment of the forms of the higher plants. A book of the highest importance not only to botanists but to biologists in general.

NEW AND STANDARD HAND-BOOKS ON AGRICULTURE, ETC.

Elements of Agriculture, Southern and Western. By W. C. WELBORN, B.S., M.S., M.P.A.

Cloth, xvi+329 pp., illus., appendix, glossary, index, 12mo, $.75 net.

NOTE.—This is a thoroughly modern treatise on farming as practiced in the Gulf States, from the point of view of the scientific agriculturist. It is adapted to school use, but is of practical service to any farmer in that part of the country. The author is vice-director of the Texas Experiment Station.

Re-issues of the highly valued Hand-Books known as the Garden Craft and Rural Science Series, edited by L. H. BAILEY, of Cornell University, Editor of "Cyclopedia of American Horticulture," "Cyclopedia of American Agriculture," etc.

The Principles of Fruit Growing. By L. H. BAILEY.
Tenth Edition, $1.50 net, by mail $1.66.

Irrigation and Drainage. By F. H. KING.
Fifth Edition, $1.50 net, by mail $1.68.

Principles of Vegetable Gardening. By L. H. BAILEY.
Sixth Edition, $1.50 net, by mail $1.68.

Bush Fruits. By FRED W. CARD.
Fourth Edition, $1.50 net, by mail $1.66.

Fertilizers. By EDWARD B. VOORHEES.
Tenth Edition, $1.25 net, by mail $1.38

Farm Poultry. By GEO. C. WATSON.
Sixth Edition, $1.25 net, by mail $1.42

Published By **The Macmillan Company** 64-66 5th Ave., New York

THE
AMERICAN NATURALIST

VOL. XLIII *November, 1909* No. 515

THE AMERICAN TOAD (BUFO LENTIGINOSUS AMERICANUS, LECONTE)

A STUDY IN DYNAMIC BIOLOGY

NEWTON MILLER

CLARK UNIVERSITY

INTRODUCTION

FOR some years it has been my desire to inaugurate a series of university theses aimed distinctively at studying important American species as forces in nature. This kind of work has seemed to me logically the next step in the advance of American natural history. In fact, it is hard to imagine any other line of real advance possible. Species are not discovered, determined, named and classified for the mere sake of making it possible for people to learn their names.

No matter how common the species, when we ask the questions: What does it do in the economy of nature? What position does it occupy in the vital organization of American natural history? What are its relations to human interests? In short, what expression have we of the species as a force in nature? When we ask these questions of the commonest animals, we find ourselves almost as near the verge of human knowledge as with an undiscovered species. No less a man than Darwin himself led off in the field of dynamic biology with his study of "Earthworms and Vegetable Mould." A

large number of living forms await study from a similar point of view.

If we determine accurately the work of an individual and multiply this by the number of individuals, we have an expression of the species as a force in nature. Hence it is true, in general, that the commoner or more numerous a species is, the more important its biological work. We accordingly begin this series of dynamic studies with one of the commonest of American animals.

Of the ten species of Bufonidæ now recognized in the United States *B. l. americanus* has the widest range, which includes almost the entire continent of North America east of the Rocky Mountains. It is, therefore, probably the most valuable type of the group.

The insect problem, further, is one of the most important in the entire field of American natural history. It finds partial expression in the annual tax of $795,100,000 which insects impose upon our agricultural resources. This is a rigidly conservative estimate made by the department of agriculture and does not include costs of abating annoyance or losses of household goods or those occasioned by spread of human disease. A large proportion of this loss might be most economically prevented by a reasonable knowledge and utilization of insectivorous animals. With all our books, bulletins and talk about it, we have scarcely made a practical beginning in this direction as a people.

In seeking animal allies to aid in the solution of the insect problem we should choose those which will do the work required most effectively and at the same time present the fewest objectionable features. A good many birds are efficient destroyers of insects, but become injurious if their numbers are unduly increased. Many insects are parasitic and predaceous, but, in general, their breeding or regulation is beyond human control. Clearly an animal to be depended upon to hold insects in check should be one which man can breed in any desired numbers and, on account of the enormous reproductive possibilities of insects, a form which he can in-

crease rapidly. We may do much by way of increase of insectivorous birds, and even bats may prove valuable allies. We may be grateful for the help of predaceous and parastic insects, and good work has been done in importing parasites of foreign insect pests, but clearly we need all the assistance we can find; and all the above agencies are scarcely controllable enough to be depended upon.

For an insectivorous animal which conforms to every requirement of the situation, ease of control and rapid increase, non-injurious, in any numbers, an active feeder in abundance and a patient faster in scarcity, the toad stands probably first on the list among American insectivorous animals. Experiments are now being carried on also with the bob white or American quail with every prospect that this form may prove of equal, if not superior, efficiency, and it will carry added values, in food, sport and weed-seed destruction; but this species is rapidly being exterminated from a large portion of its former range, and it will require a long time for methods of propagation and protection to be worked out and become generally known.

A good deal of unnecessary balancing of accounts has been done of late in attempting to calculate the economic value of species from analysis of the foods. In some cases this has yielded results of some value, but, in general, they have been misleading. Even a small percentage of the gross food of a hawk or shrike, for example, if it consists of a valuable species, might render the predaceous species injurious. In the case of beneficial insects, excepting the honey bee which is under human control, if a species will destroy all the injurious insects, it detracts little or nothing from its efficiency, if it take the beneficial insects as well. This principle applies particularly to the toad, which takes everything in the form of an insect, worm or slug that comes in its way.

Instead of filling its stomach four times in twenty-four hours, as Kirkland estimated, Mr. Miller finds that the toad takes but a single meal a day. This is no discredit

to the efficiency of the species. It means, simply, that we should require four times as many to do the work, and, with the number of eggs produced, this offers no difficulty.

Given a pond or even a small pool insured against drying up during the late spring and early summer, and from which natural enemies are eliminated, toads will breed in any desired numbers up to the limits of insect food supply. It would probably, however, be difficult or even impossible to find a single farm in the United States or Canada, although suffering severely from depredations of insects pests—not even the agricultural experiment station farms—which makes any provision whatever for the breeding of toads. In fact, reports so far gathered reveal the fact that farms in the agricultural states of Indiana, Ohio and Illinois are almost entirely destitute of the species. It is probably safe to infer that the toad has been exterminated already from a considerable portion of the cultivated land in the agricultural states. Is this an inevitable result of draining land, and modern methods of tillage? If this be true, can any changes or adjustments be made which will permit the increase of the species? Will the value of the toad's work warrant anything of the kind? Would it pay to establish special breeding places like our present fish hatcheries, or possibly in connection with them?

In order to answer these and many other questions we must have the data of the life and work of the species. To gather these in a manner, if possible, complete enough to serve as a guide and basis for practical action is the purpose of Mr. Miller's work.

THE AMERICAN TOAD (*Bufo lentiginosus Americanus* LeConte)

The ancestors of the Bufonidæ first appear as fossils in the Oeningen beds below the Miocene Tertiary strata. The group now has a wide range, being found in all parts of the temperate and torrid world with the exception of Australia and the oceanic islands. The greatest number of species is found in the torrid regions. The

Bufondiæ are represented by nine genera and more than a hundred species. Bufo takes its origin in the Sonoran subregion, *i. e.*, the southwestern part of the United States. It is the only genus found in the United States and is represented by ten species, most of which belong to the southern states. The species *lentiginosus* and its varieties are found throughout the eastern part of the United States and Canada. Two varieties, *americanus* and *fowleri*, share this region (Massachusetts).

Jordan and Cope class the American toad along with Fowler's as a variety of *Bufo lentiginosus*.[1]

My object in this work is to give as completely as possible the entire life and work of one species as normally lived in its own environment. Observations were made continuously throughout the year on the species, *Bufo lentiginosus americanus*, the results of which are given under the heads, Spawning Habits and Seasons; Development, Habits, and Food; Hibernation; and Enemies.

I am indebted to Dr. C. F. Hodge for suggestions while collecting the data for this paper, also for valuable criticisms of the manuscript. He also kindly consented to write the introduction. I wish also to thank Mr. F. E. Chidester for assisting me with the feeding-tests and in obtaining data on the daily life of the toad.

Spawning Habits and Seasons

Observations were made for the springs of 1907 and 1908, but if not otherwise stated the data for this chapter refer to the spring of 1907. Mention is made of 1908 when this season varies from that of 1907.

Toads were first seen in 1907 on the twenty-eighth of March and on the thirteenth of April in 1908. An adult male was found in the water on the night of March 29, 1907, but was so numb that he could not give the usual chirp when picked up. From March 29 to April 21 there was a decided drop in the temperature and toads

[1] More recently Miss Dickerson has given these toads specific distinction, *i. e.*, ***Bufo americanus*** and ***Bufo fowleri***.

were not seen again until the night of the twenty-second of April, on which date seven males were found trilling in pond no. 1.[2] Eight days later when the migration to the ponds reached its maximum, mated pairs were abundant on the streets and elsewhere on their way to the water. Trilling began in 1908 on the twenty-third of April and spawning on the twenty-fifth, ending May 13.

The seven toads mentioned were the first heard trilling this season. They were sluggish and when taken up between the thumb and finger could not chirp, although they made the attempt.

The accompanying curves show the number of toads as well as the number of males and females that were found in pond no. 1 on the night of April 24 and succeeding nights (Fig. 1). Spawn was found here the twenty-

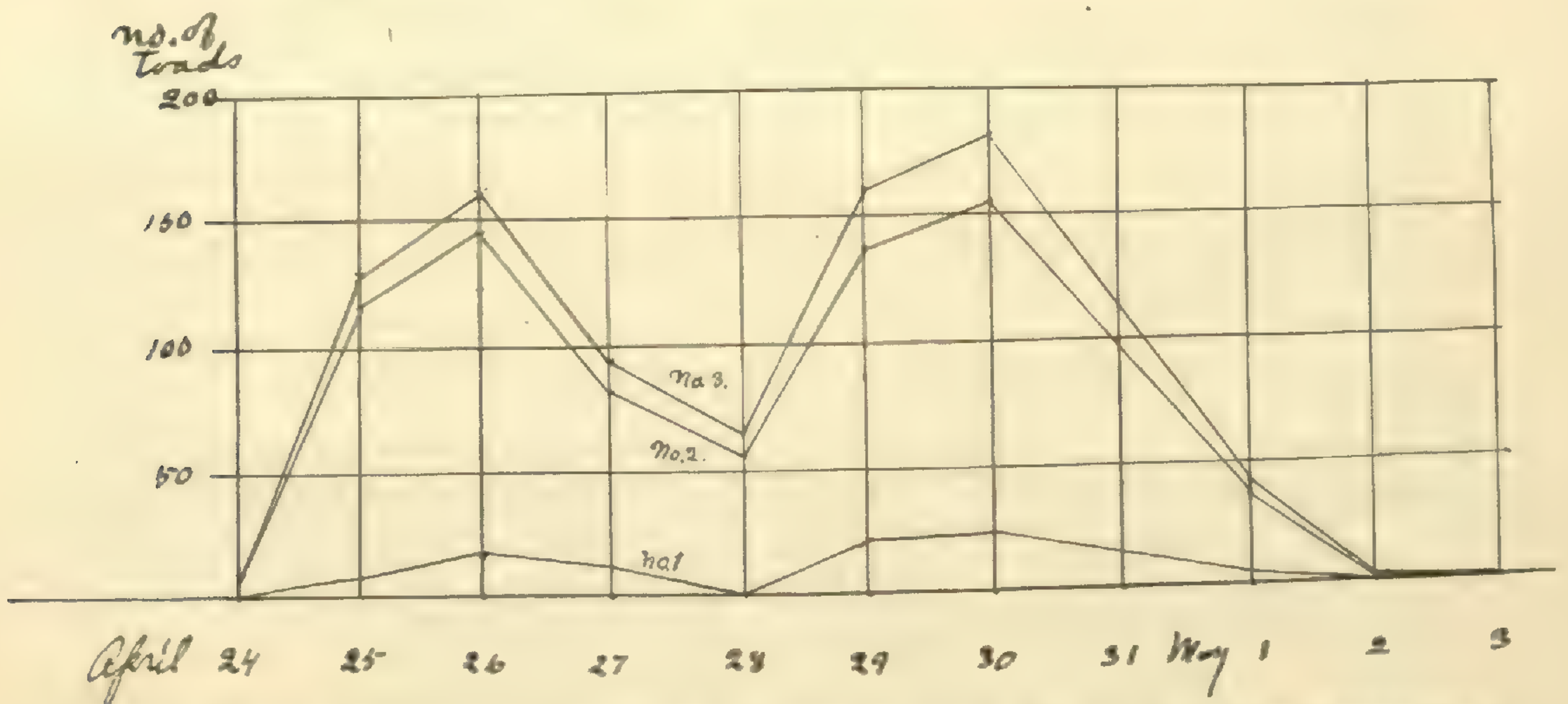


Fig. 1. Curves showing the number of toads in pond, No. 1, during the spawning season. No. 1, Females. No. 2, Males. No. 3, Total.

sixth. The males were most active on this and the night of the twenty-ninth. On these dates they were trilling vigorously and actively swimming about. If they saw an object moving they swam to it with all possible speed. When it was a male, which was usually the case, he was seized, but loosed as soon as he chirped. They even came

[2] This pond is located at the foot of a small steep hill in a pine grove in Park Avenue Place within a hundred yards of a large permanent pond. It is V-shaped, not more than fifteen feet wide by fifty feet long, and during the spawning season was about eighteen inches deep. For the most part it is filled with leaves, some water plants and debris from a near-by dumping ground. Rains are its only source of supply and it goes dry in summer.

to me as I waded out or made a disturbance in the water. All the females on the night of the twenty-seventh and succeeding nights were removed from the pond to the laboratory.

To sum up my observations on this pond we find: first, that the males are the first to reach the water; second, that there were two waves of spawning activity; third, that not less than ninety-two females visited this pond; fourth, that on an average 88.8 per cent. of the toads in the water at any given time during the spawning season were males.

Of eighty-two taken at random from the streets after the breeding season 60.8 per cent. were females. Kellicott gives the proportion of males to females of those collected along Lake Erie, Ohio, as 175:266; King for toads near Bryn Mawr, Pa., 713:823; *i. e.*, 39.7 per cent. 46.5 per cent., respectively, were males.

The females leave the water as soon as they spawn (from six to eighteen hours after reaching the pond). It is probable that the males return to the ponds night after night, which accounts for their apparent excess in numbers during the spawning season.

Observations were made on five ponds, and it was found that the periods of maximum spawning were not simultaneous in all. In no. 1 and no. 2,[3] the spawning period reached its maximum on the nights of April 29 and 30; in no. 3,[4] May 1 and 2; in no. 4,[5] May 14 and 15; in no. 5,[6] May 18 and 19.

[3] Pond no. 2 is at the junction of Park Avenue and Maywood Street. It is a permanent pond of about thirty yards in diameter with a depth of three feet. Around its west, north and east edges is a dense growth of bushes, some growing far out into the water. The south side has its growth of flags and water grasses. To the south and west is an open field, while buildings are near to the east and north.

[4] No. 3 is an overflow of Beaver Brook in an open place just below May Street. This pond is permanent, but the water falls soon after the spring rains to such an extent that most of the spawn is lost.

[5] The pond in University Park is about thirty yards in diameter and has a depth gradually reaching three feet. Its edges are gravelly and the water plants about it are confined to lilies near the west edge. A row of trees is along the north side.

[6] The pond located in Elm Park is a permanent, walled body of water

Why should there be this difference of twenty days between the spawning periods of toads in no. 1 and those in no. 2? It can partially be explained by a cold wave which set in on the fourth of May and stopped laying until the ninth. Even so, the toads in no. 1 had finished spawning before the cold wave came. Neglecting the five days of cold weather, there still remains a difference of fifteen days. These ponds are not more than a mile and a half apart. The elevation is practically the same, also the surroundings. Therefore the environments of the two ponds do not seem sufficiently different to account for so much difference in the spawning periods.

My observations indicate that toads proceed to the ponds immediately after emerging from winter quarters. If this be true, then there is a second laying, or some toads do not come from hibernation until late in June. Observations on one toad in my experiments on hibernation suggest that the latter is true. This female came out for the first time May 28, and if she had gone to the water at once, she would have been thirty-three days later than the first that spawned. I might add that I have seen no large toads among these late layers. All the females are about forty grams or less in size.

The bulk of the spawn for the spring of 1908 was laid in all the ponds between May 2 and 6. A minor period of spawning occurred on the eleventh to thirteenth.

The first few warm days of spring bring out the toads and soon the males are heard in the ponds. In a few more days the females follow and spawning begins at once. I have seen no toad eggs in running water, although there is a small stream within less than two hundred feet of ponds where many toads spawned. However, Dr. Hodge informs me that toads spawn in Rock River, Wis., and Ottawa River, Canada, and Mr. Morse states that toads generally spawn in small streams in Ohio. Toads in this region prefer small ponds in which

about two hundred yards long by twenty wide. Its depth is probably three feet. Trees surround it and a three-hundred-foot hill rises at its west side. Buildings skirt all sides of the park except the west.

to spawn. Pond no. 1 is within a hundred yards of a large permanent pond, and when there were a hundred or more toads in the former, very few were to be found about the latter.

In natural ponds toads congregate more or less during the spawning season and in a given pond 90 per cent. or more of the eggs are laid within a radius of fifteen feet. In three of the four natural ponds observed the eggs were deposited in an area less than fifteen feet in diameter. Other places similar to those where the spawn was laid existed in these ponds, but were used only by a very few toads if at all. Usually only a portion of the grassy place chosen was used (Fig. 2). The artificial pond in

FIG. 2. Pond No. 1. Circle shows the spawning place.

University Park gives almost the same results. Here the edges are kept clean and the toads had to deposit their spawn on the bottom. Nevertheless, all the eggs laid here before May 4 were deposited in an eight by ten foot strip of the north shore.. Later, May 9–15, eggs were laid all along the north and northeast sides, with a few scattered spawn along the south. The two or three

pairs that may occasionally be found in ponds during the latter part of May and June may deposit their eggs any place about the ponds. I found a little colony of some twenty pairs June 4–8 laying in a space not more than six feet in diameter in an overflow of Beaver Brook. My observations for the spring of 1908 on the same ponds confirm the above statements. The spawn in the various ponds was deposited in almost exactly the same places as the previous year.

Since in general only limited areas are used for spawning it would indicate that there is some choice among toads for spawning grounds. This is done by the males, but without the purpose of having the spawn deposited in such and such a place. They reach the water two or three days before the females and begin their trilling. They seek out each other and repeatedly attempt copulation with one another. In this way all the males in the pond are soon brought together. Even a day or two before the females arrive they are assembled, usually, on some grassy spot out in deep water, to which they return after a fruitless attempt to mate with other males. The females, following the trill of the males, come at last to this circle where they mate and lay. Thus these resting places of the males eventually become the spawning grounds. The observations of Mr. Courtis, later repeated by myself, support the view that the females come to the males.

The spawning place is usually a grassy plot well out in the pond where the dead grass or weeds come to within two or three inches of the surface. In artificial ponds where such places do not exist a shallow place along the edge is used. In the former case the female, as a rule, does not go down to lay, while in the latter practically all spawning is done under water.

Should it turn cold while the toads are spawning they leave the water until the temperature again rises. Meanwhile, they may be found concealed in the grass or leaves, or sunning themselves at the edge of the pond, often the

male still clinging to the female with which he had mated before leaving the water.

As with all amphibians the eggs are fertilized outside of the body. In mating the male clasps the female just back of her fore legs and then places his hind feet upon her thighs. This is the position maintained throughout except at intervals during oviposition. The intervals are about fifteen minutes apart. At such times the female straightens her body, raises her head, and stretches her hind legs backwards. The male hooks his feet between the female's hind legs, thus forming a basket between the feet and legs of the male and the legs and body of the female. (Fig. 3.) In this basket are now

FIG. 3. Shows the formation of the basket in which the eggs are fertilized.

deposited probably two or three hundred eggs, while simultaneously the male ejects his sperm. Boulenger is no doubt mistaken in the purpose of this process when he writes that the male (*B. vulgaris*) aids the female in

oviposition by pulling the eggs strings with his toes. That the male ejects his sperm at this time was demonstrated by microscopical examination of a slide applied to the anus of the male just before and during oviposition. In the former case, very few if any spermatozoa were found, while, in the latter, they were found in abundance.

As soon as the eggs and sperm are ejected the toads remain quiet, holding the mass in the improvised basket perfectly quiet from one to three minutes. This is ample time for the spermatozoa to get well attached to the eggs, since fertilization takes place within four minutes from the time the eggs leave the oviduct. The female now moves along, stretching out the strings of eggs just laid.

Most of the eggs are deposited in water not more than ten inches deep. Those found in weedy and grassy places are, usually, not over four inches under water. In University and Elm Park ponds where the toads were much disturbed, a large number of eggs was deposited some distance from the edge at a depth of eighteen inches or more. This deep laying seemed of no particular disadvantage, since a toad can remain underwater as long as fifteen minutes, which is ample time to fertilize the eggs and stretch out the egg strand.

The eggs are encased in a continuous, cylindrical, gelatinous strand of three to four millimeters in diameter. The gelatinous coat is added in the oviduct, and as soon as ejected absorbs water and swells. In this way there is a mass of .0225 gram of jelly-like substance about each egg, which serves as a means of protection. Eggs removed from the ovary weigh on an average .0024 gram and measure 1.1 to 1.2 mm. in diameter. When laid they are variously spaced in the strands even of the same spawn (Fig. 4). Sometimes they are crowded together so that as many as three may be in the same cross-section, or again regularly spaced at intervals of about 1 mm. The strings may be laid by either twos or fours. I have not observed in smaller toads (under 7 cm.) more than two strands being deposited at the same time, but in the

larger females four are not uncommon. The time required for oviposition varies between six and eighteen hours.

The number of eggs in spawns may be said to vary with the sizes of the toads. Thus females 6 cm. long lay

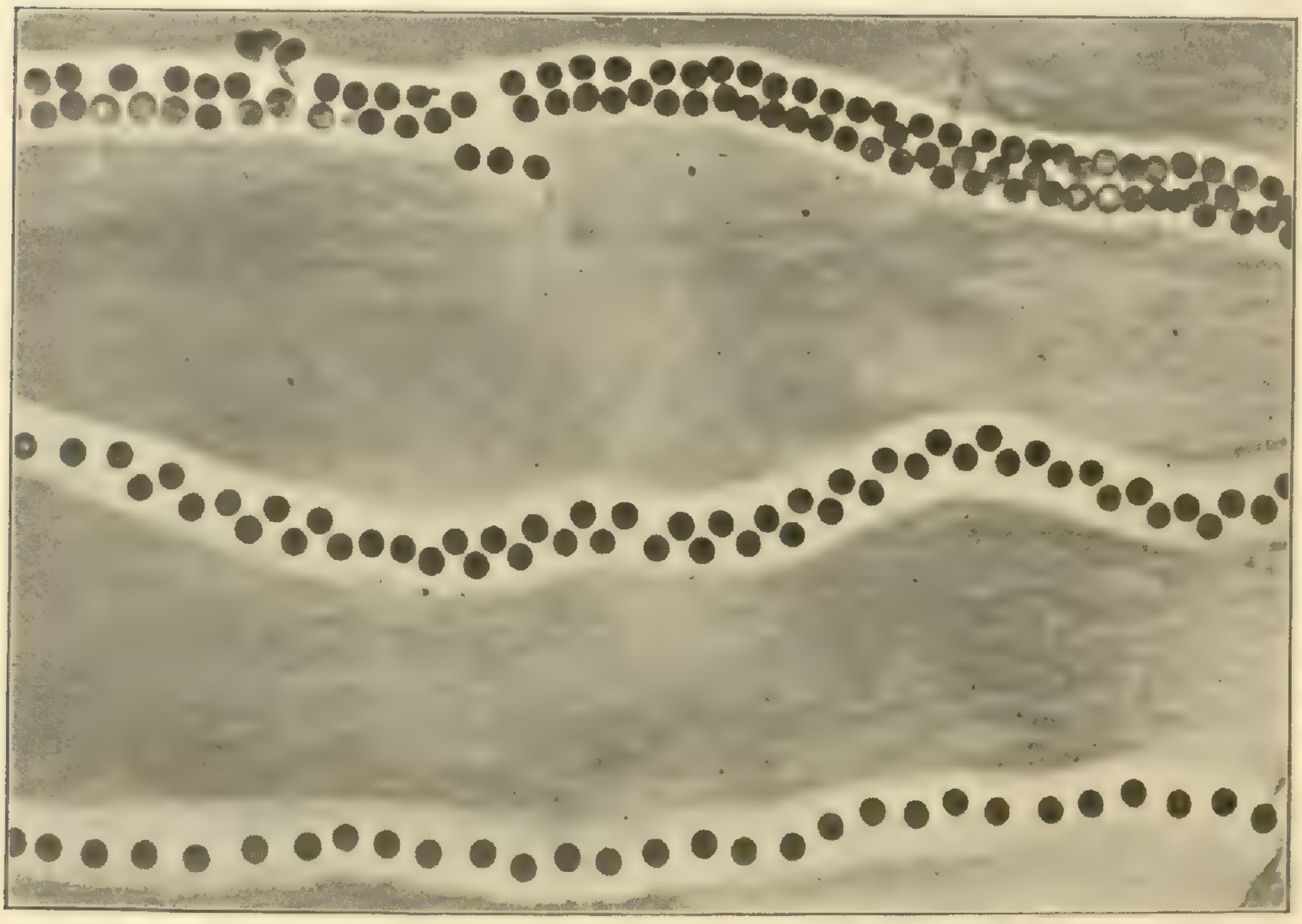


FIG. 4. Spacing of the eggs as seen in a single spawn.

about 4,000 eggs while a toad 9 cm. long may lay 15,000. The smallest spawn observed consisted of 3,929 eggs and the largest 15,835. These were laid in the laboratory.

On making some computations on the largest spawn, we find that the eggs weigh 38 grams and with the gelatinous covering, 394 grams. This latter weight is about five times the weight of the toad. Again, allowing a space of 1.5 mm. for each egg, we get 41 meters, or 134 feet as the length of the strings.

Only the males trill or make any sounds. While trilling the mouth and nostrils are closed and a pouch under the throat is inflated. Trilling in the full strong note was observed only in connection with mating. Miss Dickinson describes the call as follows:

> The sustained note is not only high pitched and tremulous, it seems to have a dual character as though a low note was droned at the same

time that the high one is whistled. Imitate the call by whistling the upper and at the same time humming the lower of the following notes:

Concerning the call of the toad after the breading season she writes:

> I have heard this feeble note of the toad in August only some half dozen times (the toads were under observation in "moss garden" in the house).

One of the toads in experiment no. II. gave this call April 5, 6 and 22. I heard at least ten toads giving this feeble note on the afternoon of the twenty-first of September, 1907, and at night of the same date just before a thunder storm. In 1908 this trill was heard as late as September 26. This note is not at all similar to that of the breeding season. It is about the same pitch but much weaker, more guttural, and not so long. The trill is not so distinct as in the spring call.

It has already been stated that on an average 88.8 per cent. of all the toads in a pond at any given time are males. Thus, for every female there are seven males. Often a male clasps a female before she reaches the water and she must carry him to the pond. At the pond a lively scene follows until the female with her mate reaches the spawning place. I have often observed two or three males clasping the same female and a few instances of four. In such cases the female is helpless and is usually held underwater. Darwin states on the authority of Dr. Günther that a female is sometimes drowned during the struggle among the males. In these contests the male always gets hold of the female, for he will not hold another male.

The one that first clasps the female in the mating position can not be dislodged, no matter how much stronger his rivals may be. The female, if she is in the water, helps her partner evade the other males by diving or sinking. This she does repeatedly and to good advantage during oviposition.

Males can not distinguish at sight males from females. For this reason they are continually clasping one another. They have a call of three or four notes which they utter in rapid succession when taken up between the finger and

thumb, or clasped by another male. This seems to be a warning signal, for a male will release another as soon as he chirps. In ponds males fight over a dead male as though it were a female. They will clasp anything moving or which touches their breast that they can hold.

It was mentioned above that spawn was deposited at a depth of eighteen inches or more in certain ponds. This depth appeared to be unusual, still the eggs developed normally. The following experiment was made with 500 eggs to test the effect of depth on hatching. One hundred eggs were placed in each of five tumblers over the tops of which were stretched pieces of cheese cloth. These tumblers were then attached six inches apart to a stick which was fastened upright in pond no. 2.

The experiment was started the twenty-first of May. The eggs in the lowest vessel developed much faster than those in the top, apparently as much as a day ahead. This can probably be explained by the fact that a cold wave came the day the experiment was started and continued for four or five days. Thus the surface was cooled more than the deeper water, but the final result of the hatching of the eggs at different depths was the same. A similar experiment made in pond no. 4 gave uniform development for eggs at depths between six and twenty-four inches. From these data it is seen that depth to as much as twenty-four inches does not affect materially the hatching of the eggs.

Counts made on eggs in various places show that 68 per cent. to 90 per cent. are fertile. On an average, development begins in 85 per cent. of the eggs.

Development, Habits and Food

The toads leave the water as soon as they spawn. Development proceeds rapidly in the eggs from which tadpoles emerge within two to six days, depending upon the temperature. At this time the larva is about 3 mm. long without mouth or appendages. On the under side of its head behind the buccal area are two small crescent-like depressions known as "sucking disks." These are

glands, however, and it is by their sticky secretion and not by suction that the tadpole attaches itself to objects.

For a day or two after hatching the tadpoles cling most of the time to the gelatinous strings or near-by plants. The tail is noticeably compressed on the second day and

FIG. 5. Toad tadpoles feeding on a pout in a natural pond.

the larva makes excursions from time to time, eventually reaching the shallow water. The mouth is formed in three to seven days, and the larvæ begin feeding. Henceforth the tadpole is a voracious feeder, living largely upon the slime at the bottom of the pond and that collected upon sticks and plants. Meats, fresh or putrid, are eagerly devoured and vegetable matter is also eaten. In this way the tadpoles play the part of scavengers (Fig. 5).

The first gills are external and are soon replaced by internal ones.

The first indication of transformation is the growth of the legs. They appear as small knobs or buds about the twentieth day of the tadpole's life. Both pairs grow rapidly and within ten days may be fully formed. The front legs, concealed in the gill chamber, appear suddenly a short time before the tadpole leaves the water. One is thrust out at the breathing pore and the other breaks directly through the operculum. The tadpole is now almost ready to abandon its aquatic life and within a day it may

do so. A few days previous to this time, the tail has begun to shrink and by the second day out of the water may be completely absorbed. Meanwhile great changes take place in the region of the head. The eyes become enlarged and elevated; the larval beak or jaws are lost; the mouth broadens and a tongue forms; the gill slits close and the lungs mature. The long coiled alimentary canal shortens and differentiates into stomach and intestine. The color changes from a jet black to a brownish tinge with faint spots. The skin is yet perfectly smooth. All of this growth, development and metamorphosis from the egg to the complètion of the toad may take place in thirty-two days, or two hundred, as in the case of some kept in the laboratory in a poorly fed condition.

The following table is given to show the rate of growth and development.

TABLE I

	Total Length, mm.	Body Length, mm.	Hind Leg, mm.	Weight, Grams.
April 29, eggs laid.				.0024
May 4 larvæ still in the gelatin.	3.5			
" 5 " " " " "	4.2			
" 7 " " " " "	6.0			
" 9 " out of the gelatin	7.0			
" 11 " " " " "	8.0			
" 13 " " " " "	9.2			.0157
" 15 " " " " "	10.5			.0132
" 19 " " " " "	11.0			.0199
" 21 " " " " "	12.0			.0295
" 23 " " " " "	15.0			.0385
" 25 " " " " "	17.0			.0566
" 27 " " " " "	19.5		1.0	.0901
" 29 " " " " "	22.0		2.0	.1310
" 31 " " " " "	23.0		2.5	.1561
June 2 " " " " "	22.4		2.5	.1560
" 4 " " " " "	23.8	9.5	3.0	.1460
" 6 " " " " "	23.4	10.0	3.5	.1570
" 8 " " " " "	24.4	10.0	4.0	.1680
" 10 " " " " "	25.8	10.0	5.7	.1700
" 10 largest specimen.	28.0	10.5	7.0	.2200
" 12 one transformed.	25.2	10.0	8.7	.1520
" 14 " "	10–25.0	10.0	11.0	.1020
" 18 all metamorphosed.	10.0	10.0	11.5	.0796

The weight given for the eggs is that previously determined for those removed from the ovary. To weigh the tadpoles, they were placed upon a glass slide covered with filter paper which was moistened sufficiently to keep

the tadpoles alive. The larvæ, slide, etc., were weighed, and then, removing the tadpoles by means of a dissecting needle, the slide, etc., were again quickly weighed. This method gave me the weight desired without killing the tadpoles. There was of course some evaporation and loss of water in removing the larvæ. But, since it was aproximately the same for each weight, the data are not affected to any great extent.

This table is the average weight and measurements of eighteen tadpoles which were kept in a vessel by themselves with water plants. Their food was mostly dog-biscuit with a little meat.

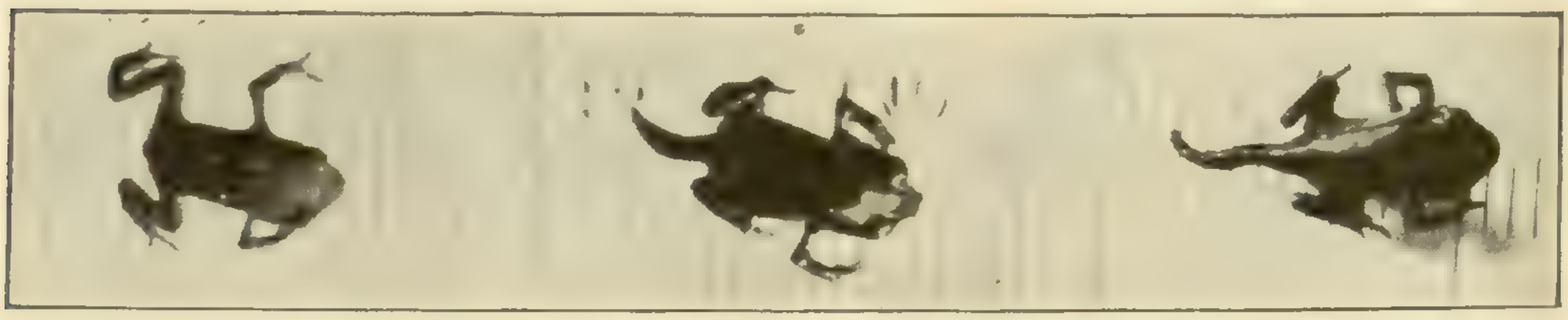


FIG. 6. Transformation. *a*, day before leaving the water; *b*, just leaving the water; *c*, day after leaving the water.

Toads just metamorphosed were seen for the first time on the morning of the twenty-third of June. During the next ten days most of the toads of the early spawn abandoned the ponds. The number leaving the water at this time is probably 90 per cent. of all that emerge during the summer. At this time eggs and tadpoles in all stages and toads just metamorphosed could be found in the same pond. Tadpoles were in the ponds as late as August 15. Larvæ from eggs laid April 29th were kept in the laboratory until October 20.

Newly emerged toads are so susceptible to transpiration that they must remain in damp places for a few days. Many remain near the ponds in the grass, under stones, etc., during the day, thereby escaping the fate of those wandering away too soon. At nights or on cloudy days during the time that tadpoles are transforming, the vicinity of ponds may be alive with young toads migrating from the water.

The great numbers that leave the water or places of

hiding during a rain, have led to the belief that toads are rained down.

After abandoning their aquatic life, these little toads simply eat, grow and endeavor to escape their enemies. By the first of October, their weight at the time of metamorphosis has been increased more than sixty times. In other words, they double in weight almost every sixteen days.

Reports indicate that toads are very unequally distributed both as to the country in general and to local areas. Killicut found them abundant along Lake Erie in Ohio. Here in Massachusetts they are very numerous. Through the northern half of Indiana toads can almost be said to be scarce, while in the southern half they are found in considerable numbers. Few were observed in the vicinity of Waterloo, Iowa. Reports from Wisconsin and Minnesota indicate that this species is well represented in these states, while in Maine and Ohio they are said to be abundant.

Toads are more numerous in and about towns than elsewhere. Very rarely is a toad seen in a large field which is under cultivation. Only fifty toads were seen during a whole season on one thousand acres of farming land in central Indiana. This scarcity may be accounted for by two factors, *i. e.*, first, that pasturing and tillage kill the toads or, second, that the extensive drainage has exterminated the toad by depriving it of breeding places. Sufficient data are not at hand, as yet, upon these two points of general and local distribution to draw conclusions.

During the summer the toad leads a solitary life and no more utters the ringing trill of the breeding season. On very rare occasions, which may be as late as September 21, he may strike up a weak, shorter and more guttural note, which is much inferior to the vigor and fullness of the mating call. This note is so rare that the toad may be considered silent throughout the summer.

Rarely, except at night or on cloudy days, is the toad seen hopping about. Late in the fall, however, he may

be found sunning himself in the grass. At this time he is sluggish and apparently only waiting for cold weather to put him to sleep. Toads come out of their hidings on rainy days, and, especially, on nights following rainy days. I counted fifty-two toads in a vacant lot between 7:00–8:00 P.M., July 22, after a hard rain in the afternoon. Counts repeated here for the next nine days at the same time in the evening varied between 0 and 16, and most of the times there were less than six toads to be seen. On the twenty-second many of this year's toads were seen, but on the following nine days, scarcely one could be found. In general, throughout the summer the toad passes the day in concealment in damp sheltered places, while the night, the toad's day, is spent in foraging.

Some of the toads in the above observation of July 22 were shedding their skins, and many appeared to have just done so. This process is frequent and often takes place immediately after the toad comes from its place of concealment.

The one in experiment IV shed her skin every seventh to eleventh day, or on an average once every 8.2 days from October 23 to April 8. Those in Experiment III did not shed so often nor as regularly; some going as long as four weeks without shedding, unless they did so in their burrows. I have seen some indications that shedding is done while the toad remains buried, and the process may be frequent and regular although the toad remains concealed.

The process is accomplished by pushing the skin forward to the neck by the hind feet and then pulling it off over the head by the fore feet. That on the hind legs and feet is rubbed off against the sides of the body, while that on the fore legs and feet is pulled off by the jaws. The skin is removed from the feet and legs in a manner very similar to that of seizing a glove by the top and turning it wrong side out as it is pulled off. As the skin is raked over the head it is seized by the jaws and swallowed. Previous to the removal of the skin, the new skin secretes

a viscid substance that loosens the old from the new and leaves the body moist for a short time after the old skin has been shed. The whole process is accomplished in about two minutes.

The following is a record of the work done by an adult male (weighing 36 g.) in twenty-seven hours. The distance traveled in this time was 85 feet, and the number of insects taken, 23. Twenty hours and five minutes were spent in burrows and, for the rest of the time, the toad was active only one hour and forty-seven minutes. It is probable that the period of activity from 7:20–8:40 A.M. would have been lessened had not another toad entered the burrow of the one under observation and forced him out. More than half of the total distance traveled in the twenty-seven hours was covered in quest of a second burrow. The following is the time spent in the burrows.

July 25, 1:50 P.M.–7:55 P.M.
July 25, 11:50 P.M.–2:30 A.M.
July 26, 4:05 A.M.–7:20 A.M.
July 26, 8:40 A.M.–4:00 P.M.

The food taken consists entirely of animal matter. Mineral or vegetable material is often found in the toad's stomach, but it is there by accident. I have found as much as 0.07 gram of coal and sand in the stomach of a 5.5-gram toad; it had just swallowed its skin and along with it the coal and sand which stuck to it. I have also seen pieces of grass, winged seeds and other bits of plants snapped up and swallowed with insects.

The amount a toad will eat in twenty-four hours seems somewhat astonishing if we were to judge from various reports. Miss Ellen M. Foskett records one feeding of a large toad as ninety to one hundred rose beetles. She also adds that "the toad showed no signs of wishing to conclude his meal." Kirkland found "the remains of seventy-seven myriapods in a single stomach, fifty-five army worms in another, sixty-five gypsy moth caterpillars in a fourth. In these cases, however, but one kind of food was present and the toads were above the usual size." He states further, on the authority of Mr. J. E.

Wilcox, that a toad ate twenty-four fourth moult gypsy moth larvæ in ten minutes; again, on authority of F. H. Mosher, that a toad ate thirty to thirty-five full-grown celery worms in three hours at intervals of about twenty minutes. Eighty-six house flies are recorded by Dr. C. F. Hodge as being snapped up in less than ten minutes. Dr. J. R. Slonaker fed an eighty-gram toad all the beefsteak and flies it would eat for two days. On the first day, December 7, it ate 2.8 grams of beefsteak and three flies; on the second, 3 grams of beefsteak and twelve flies. From further feeding he concluded that his toad would eat on an average forty flies per day.

A. H. Kirkland, H. Garman and F. A. Hartman have given us much valuable information on the food of the toad from careful analyses of stomach contents. Kirkland examined one hundred and forty-nine stomachs collected from April to September, of which he gives the following as a fair specimen. The toad was killed at 9:00 P.M. May 11, 1896, and found to contain: "9 ants (*C. Pennsylvanicus*), 6 cutworms, 5 myriapods (Julius sp.), 6 sowbugs (Parcello sp.?), 1 weevel (*Hylobius pales*) and 1 carabid beetle (Pterastichus sp.?)"; total 28. Kirkland's report shows that 84 per cent. of the toad's food consists of 28 per cent. lepidopterous insects and their larvæ, 27 per cent. beetles, 19 per cent. ants, 10 per cent. myriapods. The insects alone were represented by eighty species.

The five records which follow are those of Garman.

No. 20, a toad 1⅛ inch long, obtained on the Experiment Farm, August, 1896. 2 *Drasterius elegans*, 1 *Diabrotica 12-punctata*, 1 *Sytena tæmata*, 1 millipede (Polydesmus), 1 bug, fragments of ants, 6 chinch bugs and fragments of others.

No. 1, a toad of medium size, captured beneath an electric burner, Lexington, Ky., Oct. 1, 1894, had eaten 27 ants, 19 sowbugs, 3 spiders, 1 caterpillar, and 10 plant-lice; total 60.

No. 2, a toad 1 inch long, captured in a celery patch, Lexington, Ky., Sept. 2, 1891, had eaten 14 ants and 1 caterpillar; total 15.

No. 3, captured in a strawberry patch, Lexington, Aug. 5, 1890, had eaten 2 large ground beetles, 1 tiger beetle, 1 corn root-worm beetle, 1 lady beetle, 8 small ground beetles and 9 ants; total 22.

No. 4, taken Lexington, July 26, 1890, had eaten 2 Colorado potato

beetles, 1 click beetle, 4 bugs (Cydnidæ), 1 tiger beetle, 1 moth, 7 ground beetles, 6 ants, 1 millipede and 1 sowbug; total 24.

The above data on six stomachs are given in order to show what a toad feeds upon while in its natural habitat. So far as known a toad will eat any arthropod, mollusc or worm that it can easily swallow, without regard to spines, stings, noxious odor or taste. The question then is, in determining the economic importance of the toad's feeding habits, not to know how much it can or will eat, but to know, *how much it actually does eat.* Owing to the slow digestive rate of the toad, stomach examinations give us a close approximation to the desired information.

It is stated by Kirkland that a toad will fill its stomach four times per day. This seemed to me to necessitate rather rapid digestion for a cold-blooded animal, and I made the following experiment to test it.

August 8, a female weighing 35 grams was killed thirteen hours after having fed on three Colorado potato beetles and two grasshoppers. Examination of the stomach showed the beetles still entire. The grasshoppers had disintegrated, but none of the food had passed from the stomach.

August 26, 2:00 P.M., two toads, nos. 1 and 2, weighing seven and twenty-five grams, respectively, were fed chiefly on grasshoppers. Eighteen hours later, no. 1 was killed and at the end of twenty-two hours, no. 2. All of the food was still in the stomach of no. 1 but well digested. Stomach no. 2 contained a portion of the food, but most had passed into the intestine.

August 30, 11:30 P.M., a toad weighing twenty grams was fed on two beetles, two grasshoppers and one fly. When examined eight hours later the stomach showed: the grasshoppers well digested, but not disintegrated and the fly and both beetles still entire.

These tests demonstrate that a toad can not fill its stomach more than once in twenty-four hours. A toad will eat at intervals when its stomach is only partially filled, but to completely fill it four times a day is out of the question.

TEST No. I

Date. 1907.	Toad No. 1. Weight 58.		Toad No. 2. Weight 56.		Toad No. 3. Weight 24.		Toad No. 4. Weight 16.		Toad No. 5. Weight 6.4.		Toad No. 6. Weight 15.		Toad No. 7. Weight 25		Toad No. 8. Weight 30.		Toad No. 9. Weight 35.		Toad No. 10. Weight 34.	
	No. of insects.	No. of grams.	insects.	grams.	insects.	grams.	insects.	grams.	insects.	grams.	insects.	grams.	insects.	grams.	insects.	grams.	insects.	grams.	insects.	grams.
Aug. 3	40	3.5	37	3.8	60	2.8	15	1.2	29	3.0	42	3.9	30	3.0	28	3.0	27	3.2	40	3.8
" 4	60	3.7	37	3.8	2	1.2	0	0.0	0	0.0	0	.0	15	1.4	40	2.5	0	0.0	0	0.0
" 5	0	0	15	4.1	13	2.5	0	0.0	2	.11	14	1.6	18	1.3	0	.0	0	0.0	0	0.0
" 6	25	2.1	22	2.5	37	3.1	0	0.0	0	0.0	0	0.0	69	1.6	19	13	0	0.0	17	.67
" 7	30	3.0	42	3.5	27	1.4	0	0.0	11	.22	0	0.0	37	2.4	0	.0	0	0.0	0	0.0
" 8	6	1.9	36	2.6	45	3.8	0	0.0	0	0.0	0	0.0	14	1.4	0	.0	0	0.0	63	0.7
Totals.	161	14 1	189	16.0	184	14.0	15	1.2	42	3.0	56	3.7	183	10.7	113	9.1	27	3 2	130	5.1

TEST No. II

Date. 1908	Toad No. 1. Weight 71.		Toad No. 2. Weight 64.		Toad No. 3. Weight 49.		Toad No. 4. Weight 46.		Toad No. 5. Weight 50.		Toad No. 6. Weight 37.		Toad No. 7. Weight 33.		Toad No. 8. Weight 35.		Toad No. 9. Weight 26.		Toad No. 10. Weight 16.	
	No. of insects.	No. of grams.	insects.	grams.	insects.	grams.	insects.	grams.	insects.	grams.	insects.	grams.	insects.	grams.	insects.	grams.	insects.	grams.	insects.	grams
June 19	30	1.5	45	2 0	36	1.5	15	0.5	39	0.6	165	3.8	42	1.7	0.0	0.0	40	1.6	17	0.7
" 20	25	1.7	152	5.1	28	1.8	38	2 8	35	1.4	80	3.2	39	1.3	0.0	0.0	21	0.6	38 S	1.7
" 21	34	1.3	23	1.5	33 S	2.3	50 S	2.0	60 S	5.1	40 S	2.5	21 S	0.7	3.5	3.0	13	0.6	49	2.7
" 22	S	1.8	3	1.1	43	3.2		2.7	25	4.1		0.5	23	1.8	2.6	1.7		1.1	35	1.7
" 23		5.7		2.5		4.0		3.0		3.6		0.5	S	1.4		1.5		2.6		1.7
June 24	Insects could not be obtained on account of rain.																			
" 25	×	0.3	×	0.5	× S	0.0	×	0.8	×	0.5	× S	0.0	×	0.0	×	0.3	×	0.6	×	0.2
" 26		0.2		2.0		0.0		0.2		0.0		0.0		0.5		0.1		0.0		1.0
" 27	S	0.0	S	0.3		0.0		1.2		0.0		0.1		0.0		0.2		0.0		0.5
Totals.		12.5		15.0		12.8		12.2		16.3		10.6		7.4		6.8		7.1		10.2

Test No. III

Date. 1908.	Toad No. 1. Weight 49.		Toad No. 2. Weight 50.		Toad No. 3. Weight 45.		Toad No. 4. Weight 40.		Toad No. 5. Weight 33.		Toad No. 6. Weight 34.		Toad No. 7. Weight 28.		Toad No. 8. Weight 24.		Toad No. 9. Weight 27.		Toad No. 10. Weight 42.	
	No. of insects.	No. of grams.	insects.	grams.	insects.	grams.	insects	grams.	insects.	grams.	insects.	grams.	insects.	grams	insects.	grams.	insects.	grams.	insects.	grams.
July 23		3.0		3.5		0.5		0.3		1.3		1.5		2.0		2.5		1.6		2.1
" 24		2.0		2.7		0.2		0.6		1.1		1.5	S	1.6		D		D		0.0
" 25		D		D		0.5		0.9		D		0.0		2.4		D		D		D
" 26		0.0		D	S	0.0	S	2.5	S	0.0		2.4		4 5		3.1		D		D
" 27	S	0.2		3.6		D		2.0		2.1	S	1.2	S	3.7		2.5		2.5		2.7
" 28		0.8		D		D		1.8		D		0.0		D		D		1.9		2.0
" 29		D		4.6		D		2.0		1.6		1.7	S	2.4		D		D		1.6
" 30		0.6		D		D		D	S	1.0		0.4		D		1.2		1.5		1.5
" 31		D	S	2.0		D		0.2		0.5		0.0		1.8		D		D		2.0
Aug. 1		D		D		D		0.8		D		1.6		D		0.5		D		D
" 2		D		D		D		D		D		D		1.0		D		D		D
" 3		0.8		D		D		D	S	D	S	1.8		0.4		D		D		D
" 4						D														
" 5						D														
Totals.		7.4		16.4		1.2		11.2		7.6		12.1		19.8		9.8		7.5		11.9

Average amount eaten per day, 11.2 grams.
Average weight of the toads, 36.6 grams.
Average amount eaten per day per toad, 1.12 grams.

S = times toads were observed shedding their skins.
D = days toads remained buried.
0.0 = days toads refused to eat when not buried.

The results given in the following table are of feeding tests made in order to see how much and how often a toad will eat. The tests were made with sweepings and, as grasshoppers formed the greater part, the experiment was carried on largely with them. This, I think, does not affect the experiment to any great extent, since toads show very little preference, if any, for certain species of insects. If toads are placed in cages with sweepings, various species are taken at random, provided only that they be moving and of a size easily swallowed.

Ten toads, half males and half females, were chosen for each test. Each toad was confined separately in a glass cage ($4 \times 5 \times 7$ inches) in which was about two inches of moist earth. Throughout test no. I, insects were kept constantly before the toads. The insects were weighed and counted, then put into the cages with the toads. In test no. II the toads were allowed to feed, one at a time, in a wire cage containing insects. The cage with the insects was weighed before the toad was put in and then weighed again after the toad was removed. Allowance had to be made for loss by evaporation in determining the amount eaten. A more satisfactory cage was constructed entirely of glass for test no. III. It measured $8 \times 10 \times 10$ inches and had on its bottom a half inch of dry sand for the absorption of moisture. Evaporation from this cage was less than a gram in ten hours. Insects were placed in it and the process of weighing followed as in test no. II.

In nos. I and III the toads were not disturbed unless they were out of the earth. But in no. II they were dug up every day, if necessary, in order that they be offered food at least once.

The following are the results of the three feeding tests.

The data show that for test no. II the toads feed oftener than in the other two experiments, but that the amount eaten, in proportion to the weight of the toads, is 3 and 2 per cent. less than in tests nos. I and III, respectively.

The time represented in these experiments is equal to that of one toad for 260 days, 96 of which were passed

without feeding. In other words, a toad refuses food on 36.9 per cent. of the days. Therefore instead of a toad filling its stomach four times in twenty-four hours, according to Kirkland, it may eat (probably fill its stomach) once in a day and a half. The average amount eaten per toad per day in these 260 days is 1.12 g. The average weight of the toads is 36.6 grams, which is about the weight of the largest males or of a medium-sized female.

These feeding tests show that the amount eaten at one feeding compares very closely with the stomach contents as recorded by Garmann, Hartman, and Kirkland. Furthermore they demonstrate: (1) That the stomach of a toad is not a rubber bag with an unlimited capacity as commonly supposed; (2) that the toad when feeding, if food is abundant, soon fills its stomach; (3) that toads do not feed every day. This was suspected, since toads are seen in greater numbers on rainy nights.

Usually as soon as the toads fed they buried themselves and remained so from one to ten days. Sometimes their eyes and nostrils were left exposed. Even so, insects placed in their cages usually failed to tempt them to leave their burrows.

If we take the mean, 36.6 grams, as an average sized toad, we find that it eats on an average, 26 insects or 1.12 grams per day. Counting May, June, July and August as a toad's feeding months, it will eat in this time some 3,200 insects, or 134.4 grams.

To estimate the value of a toad's work in dollars and cents is rather difficult, since the toad eats beneficial as well as harmful insects. Garman from his data does not hesitate to class the toad with useful animals, yet he would not have us overlook the number of beneficial insects eaten. According to Kirkland eleven per cent. of its food consists of insects directly or indirectly valuable to man and eighty per cent. is either directly injurious or obnoxious. He computes on the data previously given of a stomach content that a toad is worth $19.88 per year for the cutworms alone which it destroys. He assumes that a toad fills its stomach four times a day with 6 cut-

worms and other insects for three months and that the cutworms do damage to the amount of one cent each. Granting that cutworms are injurious to the amount of one cent each and that they work four months instead of three, still Kirkland's estimate is about four times too large, for a toad can not fill its stomach more than once in twenty-four hours. Furthermore, my experiments show that it eats, on an average, only once in one and a half days. These factors give the toad a value of about $5 per year on the basis of Kirkland's estimate. Such figures may be approximately correct for greenhouses, gardens or truck farms, but on the whole I am inclined to think they are too large for farming districts.

(To be concluded)

NOTES ON THE BEHAVIOR OF THE DOMESTIC FOWL[1]

PHILIP B. HADLEY

Rhode Island Agricultural Experiment Station

During the month of February, 1909, the writer's attention was called to an interesting feature of the behavior of a buff rock cockerel kept in the poultry department of the Rhode Island State College at Kingston, Rhode Island. Having briefly described the facts of the case to Dr. Robert M. Yerkes of the Department of Psychology of Harvard University, and having been informed by him that the behavior in question was somewhat noteworthy, the writer has collected data, secured photographs, and desires to present the following description, believing it may be of interest to students of animal behavior. The point of behavior under consideration consists in the acquired habit of an adult barred rock cockerel of "working" an automatic feeder, containing bran and grain, located in one of the colony houses of the poultry department, and by this action of securing a larger amount of the grain constituent than the feeder, working by itself, would naturally be able to supply.

The automatic feeder in question is of a type manufactured by John Anderson, of Slocums, Rhode Island, and involves mainly a box (Fig. 1, *B*) containing feed, and a tray (*T*) suspended beneath it. The dimensions of the box are roughly sixteen by eleven by eight inches. The food material escapes from the box through a narrow opening at the back and bottom of the feeder, and is caught in the tray, which is thirteen inches long by seven and one half inches broad, and is suspended eleven inches form the floor. The supply of food material falling on the tray is regulated by a balance system. The tray is so

[1] Papers from the Division of Biology. No. 5. Published August, 1909.

FIG. 1.

suspended from the point *F* that, when it is lightened (consequent to feeding), it rises and simultaneously admits a new supply of food material from the box. As soon as a sufficient amount to increase the weight of the tray has fallen, the latter drops again and automatically shuts off the supply. This process of filling and empty-

ing continues as long as there is material left in the box and there are fowls to eat from the tray.

The material contained in the automatic feeder is usually a mixture of bran, wheat, and whole corn. While both the hens and the cockerel eat a fair amount of the bran constituent, they like the grain, especially the whole corn, much better. This predilection is exhibited especially by the cockerel, which attempts to obtain a minimum amount of the bran and a maximum amount of the corn. Usually there are from four to eight hens, together with the cockerel, attempting to feed from the tray at the same time. As a consequence, the grain, which is mixed with the bran, is in the tray but a short time before it is eaten, and nothing but the bran remains. When this condition has come about the cockerel proceeds to "work" the feeder. This is accomplished in the following manner.

As shown in Fig. 1, the cockerel while eating almost invariably stands at the left-hand corner of the feeder. At this point he usually feeds from the corner of the tray, while the hens feed from both sides or from the ends, some of them standing between the feed-tray and the wall, where there is a free space of ten and one half inches. As soon as the corn has all been eaten the cockerel steps back sufficiently to clear the corner of the tray, takes a few steps forward around the corner, raises its head high and gives a vigorous push or peck to the beam designated (*a*) in Fig. 1. The force of this blow usually serves to throw out the board slat which holds the food back in the box; and, as a result, fresh material falls upon the tray, the increased weight of which immediately closes this outlet from the box. As soon as more corn has fallen on the tray the cockerel hastily returns to his former position at the corner of the tray and devours as many of the kernels as possible before the hens have again cleared the receptacle of grain; whereupon the cockerel again leaves the tray and pecks the beam. The final result of this continuous performance is that the tray be-

comes so heavily stocked with the bran constituent that it will not longer work automatically, sometimes becoming so heavy that even the most vigorous pecks of the cockerel no longer serve to raise it and admit more food.

The movements of the cockerel in working the feeder are, as a whole, characterized by directness and accuracy. Occasionally, however, there is a slight hesitation in striking the beam. In such a case the bird leaves the tray and turns toward the beam, but returns to the tray before having struck, as if influenced by the thought that grain had already entered the tray or that the other birds would secure it first. This hesitation is usually followed, however, by the complete successful performance. The accuracy of the strike is noteworthy, and a deep groove has been worn on the edge of the beam at the point where the beak strikes.

The cockerel mentioned above is a fine specimen of the buff rock variety. It was hatched at the Rhode Island College Poultry Plant in February, 1908, and now measures twenty-three inches in height. The bird has been confined in the colony house (with appended yard) for about four months, and the type of behavior described had been observed about two months before it came to the notice of the writer. It thus seems probable that the bird had been in the house with the feeder accessible for about two months before the trick was learned. At the time of writing (April 5, 1909) the cockerel still has access to the automatic feeder and works it regularly every day.

Since making the observations recorded in the preceding paragraphs the writer has secured other data which show that the ability to work the automatic feeders is not restricted to the previously mentioned buff rock cockerel alone, but is also possessed by several of the hens located in the same colony house, and by another white Orpington cockerel in an adjoining poultry house. While the behavior of the white Orpington cockerel is in most respects similar to that of the buff rock, the action of the buff rock hens is somewhat different. When the

hens feed from the tray, a few of them, as has been remarked, stand back of the automatic feeder, *i. e.*, between it and the wall, a space of about ten and one-half inches. In this position the feed tray is slightly more than breast high (thirteen and one-half inches) at the top of the rim, while slightly above the head of the birds (nineteen inches from the floor and six inches from tray) runs a guide-board, eleven by two and one-half inches. This board, which really serves as a guide to the food falling from the box into the feed-tray, is so hung that if it be struck from behind outward the effect is the same as that of striking the beam (*a*) at the point designated; that is, the grain is let into the feed-tray. Striking the guide-board from before does not accomplish this result. Now it appears that several of the hens have learned the trick of operating the supply by striking from behind, with their bills, the guide-board designated above. To accomplish this the bird merely needs to raise its head from the tray and to stretch its neck slightly in order to reach the board which is sharply pecked. It appears, however, that the hens do not attempt this manœuvre so often as the cockerel performs the other. This is perhaps for two reasons: first, the hens do not care so much for the grain; and secondly, the cockerel is apparently always quite ready to save the hens the trouble of working the feeder for themselves.

How long was required for the hens to learn the trick of operating the feeder is not known; nor are any data at hand regarding the proficiency shown at successive stages in the process of learning. When the performance was first observed by the writer the technique was already perfected. It would be interesting to learn how, in the experience of the cockerel, the connection was first made between the movement of the beam and the presence of fresh corn on the tray. The matter would be easier of explanation were the action in question one which, on the first performance, could easily have been accomplished by chance, as, for instance, the case of the dog or cat acci-

dentally striking the latch when leaping or pawing at the door for admittance. In the present instance there is performed an action which requires the cockerel to leave temporarily the primary object of his attention, and to perform a manœuvre which it seems could hardly have been hit upon accidentally, while the bird was engaged in the process of feeding.

Since writing the above paragraphs the writer has made other observations which add new interest to the subject in hand. In order to prevent the buff rock cockerel from working the feeder a piece of sheet tin was nailed to the beam which had been struck. This was placed over the beam in such a way as to protect the latter on the top, where the cockerel had usually struck it, as well as on the sides. This sheet of tin extended downward to within about one-eighth of an inch of the bottom of the beam, and hung about one-fourth of an inch outside of the same. Thus the whole of the beam, except one-eighth of an inch of the lower margin, was protected from the beak of the cockerel, and it was expected that this precaution would effectually prevent all further "working" of the feeder. This result, however, was not forthcoming, for within two days after the sheet of tin had been placed on the feeder the cockerel was found to have modified his behavior to suit the new unfavorable conditions. Now, instead of attempting to strike the beam from above, as previously, he reached with his beak underneath the projecting sheet of tin, and, grasping the lower margin of the beam, bore it downward with a kind of pulling motion from beneath. This movement, it is apparent, is somewhat different from the one first described. It is, moreover, the only means by which the feeder could possibly be worked by manipulating any accessible part of beam. It is barely possible to consider the second manœuvre as a direct modification of the first, although a different part of the beam is struck, and with a different movement on the part of the bird. It is diffi-

cult to see how this second reaction could have been developed as a result of an accidental success, especially when it is borne in mind that the manœuvre was first initiated and fully perfected within two days of the time when manœuvre number one was discontinued. Whether manœuvre number two is a modification of number one, whether it arose from imitation (which is doubtful, since no person or other fowl is known to have performed the action before it was perfected by the cockerel), or whether it is the result of a chance success following random movements, the writer is not prepared to state. Notwithstanding the fact that manœuvre number two is so different from number one, it is perhaps more reasonable to assume tentatively the correctness of the first hypothesis. But this does not explain the origin of manœuvre number one, although it surely demonstrates a very effective modifiability in the behavior of the cockerel. In the present instance it is also noteworthy, perhaps, that when the first manœuvre was prevented by the presence of the sheet of tin, the cockerel did not profit by an imitation of the hens, which continued to work the feeder from behind as in the first case mentioned above.

Believing that there are certain theoretical considerations arising from the foregoing observations which would be of interest to comparative psychologists, the writer has requested Doctor Yerkes to add hereto comments that seem pertinent to the question in hand. The writer would also take this occasion to express his thanks to Mr. Roy H. Waite, Assistant in Biology, for preparing the photograph which accompanies this paper; also to Mr. Holden, of the College poultry plant, for some of the data here presented.

COMMENT UPON DR. HADLEY'S OBSERVATIONS

Neither casual observation nor systematic experimentation with the domestic fowl has furnished many instances of the type of behavior described by Dr. Hadley. Consequently his observations have considerable interest and value for students of animal behavior.

It is scarcely necessary to say that the most serious defect in this account

of the behavior of a cockerel is the lack of the history of the formation of the habit. This defect is the author's misfortune, as well as the reader's, but it is not his fault, inasmuch as the habit was practically perfect when he first observed it. To attempt to interpret the behavior in psychic terms or to point out its significance would be futile in the absence of definite knowledge of the conditions which originally gave rise to it. This is but one of the innumerable instances in which we need more facts instead of speculation.

Dr. Hadley has suggested that the connection between pecking the beam of the feeder and obtaining grain could not have been discovered accidentally. Should he succeed in proving the truth of this supposition he would make an important contribution to animal psychology, for it is fair to say that the habit arose either from "accident" or from ideas. Evidently the author himself suspects that ideas, or some other forms of psychic process, had to do with the acquisition of the food-getting act. I wish the facts were adequate to prove or disprove this possibility. They are not, in my opinion, and it is therefore out of place to discuss them from that point of view.

The reader can but wonder whether the hens which operate the feeder acquired their method of obtaining grain under the influence of imitation. The conditions apparently furnish an excellent opportunity for the experimental study of imitation in fowls.

Surely the wisest and safest, if not the most satisfying, comment which the student of animal behavior can make concerning Dr. Hadley's observations is "let additional facts appear before interpretation is permitted."

ROBERT M. YERKES.

VITALITY OF PINE SEEDS AND THE DELAYED OPENING OF CONES

PROFESSOR W. C. COKER

UNIVERSITY OF NORTH CAROLINA

ON a visit to California in July, 1908, my curiosity was aroused by the remarkable retention of the still unopened cones in *Pinus attenuata* (*P. tuberculata*) the knob-cone pine, and to a somewhat less conspicuous degree in the Monterey pine (*Pinus radiata*). Trees of *Pinus attenuata* may frequently be seen several feet in diameter and thirty or forty years old, still retaining unopened all the cones they have produced during their lives, the lowest cones circling the tree within hand's reach from the ground. As all cones are borne on new growth it is obvious that as the branches increase in thickness the peduncles of the cones must be broken loose from their connection with the wood, so as to allow the cones to be pushed out by the annual growth, or the cones will be covered as the tree develops and finally imbedded in the wood. As the cones of *P. attenuata* are narrow at the base and thus more easily caught by the annual layers, the latter alternative sometimes occurs and the cones are covered by the growth of the tree.

The cones that remain on the surface of the trunk and branches have no organic connection with the tree, and their peduncles, which are almost an inch long, may be twisted out like a cork from a bottle. It is a well-known fact that in this case the cones never shed their seeds until the tree or branch that bears them dies.

This remarkable peculiarity is exhibited to almost as great a degree by *Pinus radiata* (Monterey pine). Of this tree J. G. Lemmon says:[1]

[1] *Sierra Club Bulletin*, Vol. 2, p. 74, 1897.

Trees four and five inches in diameter may be seen on Point Pinos, still retaining every cone they have produced, circling the trunk and limbs from base to apex. Of course the lumber is perforated with holes, the channels formed by the cone-stems on their many years' journey from heart to bark.

Other species of western American pines whose cones are serotinous to a greater or less degree are *P. muricata*, *P. contorta*, *P. contorta* var. *Murrayana* (the lodge pole pine) and *P. chihuahuana*. Of *P. muricata* Lemmon says:[2] "The cones have been known to remain unopened for twenty or thirty years, then to release good seeds," but he says in another place of the cones of the same tree:[3] "They usually open at the time the leaves at the same point fall away from the stems." The *Gardener's Chronicle* for April 24, 1909, gives a good illustration of this pine showing old unopened cones, and in the same number, Mr. W. J. Bean says: "Some of the trees at Kew bear cones which must have developed more than a quarter of a century ago."

Of the eastern American pines the only ones to retain their cones unopened after maturity are the jack pine (*P. Banksiana*) of the north, the Table Mountain pine (*P. pungens*) of the Alleghanies, the pond pine (*P. serotina*) of the southern states, and *P. clausa* of the gulf coast and eastern Florida. In the case of the last species the cones may become imbedded in the wood as in *P. attenuata*.[4]

That this remarkable habit of cone retention is of use in the struggle for existence, at least under the peculiar conditions that exist in our western country, is believed by a number of observers. The explanation that is usually offered is well expressed by John Muir in "Our National Parks" page 104. Speaking of *Pinus attenuata* (under the name of *P. tuberculata*) he says:

[2] "Handbook of West American Cone-bearers," 3d ed.

[3] *Erythea*, Vol. 2, p. 160, 1894.

[4] In *Garden and Forest*, Vol. 10, p. 232, Professor C. S. Sargent remarks that cones of *P. muricata* often become imbedded in the bark, but in a letter to me he says that this "appears to be erroneous."

This admirable little tree grows on brushy, sun-beaten slopes, which from their position and the inflammable character of the vegetation are most frequently fire-swept. These grounds it is able to hold against all comers, however big and strong, by saving its seeds until death, when all it has produced are scattered over the bare cleared ground, and a new generation quickly springs out of the ashes.

This statement of Mr. Muir's implies that all or a large part of the seeds produced during the life of the tree are capable of germination when shed, and this seems to be the opinion of others (see Lemmon, as quoted above, under *P. muricata*).[5]

Now it is a well-known fact that pine seeds as a rule are very perishable (seeds of *P. palustris* will not germinate, according to my experience, the second spring after their maturity) and it is important to test by actual experiment to what extent seeds retain their vitality under such conditions. In looking over the literature I can find but one experiment that has been made to enlighten us on this point.

In 1874 Dr. Engleman collected a branch of *Pinus contorta* from Colorado (the plant being probably var. *Murrayana*, or lodge pole pine) and after keeping it four and a half years, he sent it to Professor C. S. Sargent, of the Harvard Arboretum, to test the seeds. Professor Sargent planted the seeds in 1879, and his results, as reported in *Bot. Gazette*, Vol. 5, p. 54, 1880, were as follows:

[5] The reference to *Pinus radiata* by Vernon Bailey on page 34 of C. Hart Merriam's "Results of a Biological Survey of Mount Shasta, California" (*North American Fauna*, 16, 1899) would indicate that its seeds have a hard time on Mount Shasta. He says:

"The trees were loaded with cones, in whorls of three to seven around the branches, and down the trunks to 10 or 12 feet from the ground. Some of the cones must have been 20 or 30 years old, and perhaps much older. I cut off a lot of the old lower cones to see if the seeds were good, and put them on a boulder and cracked them with a few hard blows of the ax. All of them were full of worm dust, with only now and then an undiscovered seed or a fat white worm. Cones of medium age (5 or 6 years back from the end of the branch) were invariably occupied by worms and worm dust, and usually contained few good seeds. Cones only 1 or 2 years old were rarely wormy. A great many of the old cones had been dug into by woodpeckers, either for seeds or, more likely, for the fat white grubs that live on the seeds."

Seeds of 1865 and 1868 did not germinate.
1869 .... 24 seeds planted, 4 germinated.
1870 .... 25 seeds planted, 4 germinated.
1871 .... 6 seeds planted, 2 germinated.
1872 .... 19 seeds planted, 5 germinated.
1873 .... 9 seeds planted, none germinated (cones probably not mature).

This experiment shows that at least some of the seeds of *P. contorta* (var. *Murrayana?*) are capable of germination after retention in the cones for nine or ten years.

My interest having been aroused in this subject while in California, I was led to observe more closely the cones of our native *P. serotina* on my return to South Carolina and it was soon found that the cones of this species often remain attached and unopen for a much longer time than ever reported. In his "North American Silva," Vol. 3, p. 117, Michaux says:

> The cones arrive at maturity the second year, but do not release their seeds before the third or fourth.

Sargent follows this statement in his "Silva" and Britton says (in "North American Trees") that the cones "remain closed for several years before dropping the seed." In the neighborhood of Hartville, South Carolina, it was not at all uncommon to find cones that had remained unopened for ten or even more years, and the opportunity was taken to collect cones of different ages for a test of the viability of the seeds. The cones were taken to the New York Botanical Garden and there the test was made in June of this year. Seeds that were obviously blasted or dead (as shown by floating in water) were discarded, and are recorded as "rejected"; only apparently sound seeds were planted. The seeds were first germinated between filter paper in *Sphagnum* moss for about five days until the radicals appeared. A count was then made and the result recorded in the columns of June 29 in the table below.[6] All the seeds, whether germinated or not, were then planted in soil in pots, and

[6] Cone No. 1 was not included in this count because its seeds were by mistake planted in soil before the count was taken.

the seedlings that appeared were counted on July 12[7] and July 22, with results as shown in the table below.

Years Old.	Rejected.	Planted.	Germinated. June 29.	Germinated. July 12.	Germinated. July 22.
3	31	32	1	27	28
4	10	14	6	9	9
4	6	15	13	9	9
6	7	57	30	40	39
6	0	62	52	51	52
6	7	60	58	53	48
7	3	88	42	50	44
8	7	49	10	34	33
8	5	27	2	15	18
8	3	42	0	31	33
9	5	34	3	2	0
9	2	31	10	16	7
14	32	61	33	24	21
14	2	67	7	11	11

Increased numbers in the later readings are due to delayed germinations: decreased numbers to failure to emerge or to damping off after emergence.

It should be noted that the conditions that exist in these serotinous cones are almost ideal for the preservation of the vitality of the seeds. While some exchange of gases is allowed, the spores of fungi and bacteria are effectually excluded; and most important of all, a sufficient humidity is maintained to prevent a fatal dehiscence. That this humidity is due to contact with the moist wood of the live tree is shown by the mechanical opening of the cone through drying when it is removed from the wood, or when the tree dies. This opening, however, is not always either prompt or complete.

[7] This counting was, in my absence, kindly made by Mr. Fred. J. Seaver.

THE AFFINITIES OF THE ECHINOIDEA

AUSTIN HOBART CLARK

The recent discovery that the crinoids in their ontogeny increase the number of their ambulacral post-radial ossicles by the interpolation of numerous ossicles (in pairs) between the first two primitive brachials and the radial, forming what are known as "interpolated division series," as well as by the addition of brachials in a linear series at the growing tip of the arm, where only heretofore addition to the number of the brachials was supposed to occur,[1] has shown that in the manner of increase of the number of ambulacral segments there is a close similarity between the crinoids and the echinoids, both groups adding new plates between those already formed and the radials (oculars), whereas in the ophiuroids and the asteroids new plates are added only at the tip of the arms, not, however, at the extreme tip, as in the crinoid arm, but just proximal to a permanent plate; and the question naturally arises, can the commonly accepted view regarding the interrelations of the various classes of the Echinodermata be maintained in the light of the present state of our knowledge?

So long ago as 1821 J. S. Miller remarked on the similarity of an inverted Cidaris to a crinoid, and this similarity was also noticed by Lovén. That this similarity is not superficial but in reality fundamental has become increasingly evident to me during the course of my studies on the echinoderms, and I have now no hesitation in stating that the crinoids and the echinoids have much more in common, and are much more closely related to each other, than either group is to the asteroids or the ophiuroids.

Considering only the external skeleton, we find that, in the crinoids and echinoids (1) the ambulacrals in-

[1] *Proc. U. S. Nat. Mus.*, Vol. 35, No. 1636, pp. 113–131.

crease by the addition of plates proximally between the youngest plate and the radial (ocular); no permanent terminal plate is present; (2) the ambulacral plates always alternate in position; (3) the so-called infrabasals are inconstant (crinoids) or entirely wanting (echinoids and many crinoids); (4) imbrication of ambulacrals is more or less constant; (5) the ambulacrals are on the surface, so that the nerves, water vascular system, schizocœl, etc., are on the inner side, protected by them; (6) there are no definite or constant accessory plates in the ambulacral system; (7) the oral skeleton, when present, can not be directly derived from the ambulacral system; (8) the interambulacral plates are in more or less regular columns; but they always start from a single plate; (9) the interambulacral plates extend laterally outward from the ambulacrals, forming a closed capsule; (10) the plates of the ambulacral system encroach regularly, when at all, upon the peristome, which remains round; (11) the spines are long and usually slender, and are attached to round and prominent spine bosses (present among crinoids in one genus only); (12) the ambulacrals are directly continuous with, and in the same plane as, the radials (oculars): on the other hand, in the ophiuroids and asteroids (1) the ambulacrals increase by the addition of plates distally between the youngest plates and the permanent terminal; (2) the ambulacrals are always opposite each other (a possible exception in certain palæoasteroids); (3) the infrabasals are ontogenetically constant; (4) there is no imbrication of the ambulacrals; (5) the ambulacral ossicles lie deep, so that the radial structures are outside of them; (6) definite and constant adambulacral ossicles or lateral shields are present; (7) there is a peculiar oral skeleton of modified ambulacral plates; (8) the interambulacral plates are in regular rows, starting as some multiple of two; (9) the interambulacral plates enclose more or less the ambulacral plates; (10) the plates of the ambulacral system encroach irregularly upon the peristome, making it more or less sharply stellate; (11) the ambulacral plates

never bear spines; (12) the ambulacrals are not continuous with, nor in the same plane as, the so-called radials or terminals.

This would be sufficient in itself to convince any one that the crinoids and echinoids formed one well circumscribed group, while the asteroids and the ophiuroids formed another similar group, entirely distinct; but the "soft parts" furnish abundant additional evidence leading to the same conclusion.

In the urchins and the crinoids the anus is always well developed and functional, while in the asteroids and ophiuroids it is absent, or, if present, does not serve as an exit for refuse matter; the crinoids and urchins have a large and definite peristome which is circular in shape and more or less filled with dermal plates; in the asteroids and ophiuroids the peristome is very much reduced, stellate and without dermal plates; in the crinoids the ambulacral plates are united by ligaments externally and by two parallel rows of muscle bundles internally; in the echinothurids, which alone among the echinoids have a flexible test, the plates are united by more or less ligamentous connective tissue, and within the test there are five pairs of muscle sheets, inserted along the two outer edges of the ambulacral series; the asteroids and ophiuroids have two pairs of muscles, a dorsal and a ventral instead of one pair and a dorsal (external) ligament. In the crinoids and echinoids the intestinal canal is narrow, tubular, without marked sac-like expansions, and always lies in coils of which there may be as many as four; in the asteroids and ophiuroids the digestive system runs direct from the mouth to the anus (when present) without convolutions, but has sac-like widenings, and may have branched radial outgrowths. In the crinoids and the echinoids the gonads are connected with the axial organ in the young, but not in the adult; in the asteroids and ophiuroids they are connected with the axial organ throughout life. In the echinoids and crinoids the pseudo-hæmal system is closed on all sides; in the asteroids and ophiuroids it connects by means of numerous

small apertures with the body-cavity, and, at one point in the pseudo-hæmal ring, with the axial sinus. A blood vascular system is doubtfully present in the ophiuroids and asteroids, but well developed in the echinoids and crinoids. In the echinoids the axial sinus surrounding the stone canal, originally a part of the cœlom, is in open communication with the ampulla into which the madreporite opens. This is comparable to the condition in the crinoids where the madreporic pores open into the body cavity more or less opposite the openings of the stone canals, but is quite different from the condition found in the asteroids and ophiuroids.

Having now shown that the crinoids and the echinoids are closely related, it remains to be seen how an homology may be drawn between the skeletal elements of the two. This is not nearly so difficult a performance as might appear at first sight. The primibrachs of a crinoid represent the first four ambulacral plates of an urchin, which have slipped in between each other so as to lie in a single row; in this single row of four plates the second has disappeared, as shown by the synarthry,[2] while the third and fourth have united to form an axillary. All the plates in the crinoidal post-radial series up to the third brachial of the free arm represent the ambulacral series of the urchin; the long and tapering crinoid arms from the third brachial onward are homologous to the auricles and apophyses of the urchin, which have become turned outward instead of inward, have become interiorly united, and have increased enormously in length. The crinoid stem is the central (sur-anal) plate of the urchin; originally free, the crinoids first became sessile through simple attachment by the central dorsal plate; this gradually increased in thickness, becoming a thick stalk, like that of Holopus; later, owing to the increasing length, fractures were developed transversely, and finally the long jointed crinoid stem resulted.

It has been urged, from their radiate structure, that the echinoderms were primarily fixed; but I can not see

[2] AMERICAN NATURALIST, Vol. 43 (October, 1909), pp. 577–587.

why the octopus could not be assumed to have been descended from stalked ancestors along the same lines. It seems to me that the echinoderms are rather like the bivalve molluscs or the crustacea which contain both free and fixed types, the former in the great majority. The crinoids are the only recent fixed echinoderms; but in the fossil crinoids, as Lang pointed one in Marsupites and I independently showed in Uintacrinus, there are forms which exhibit no evidence of ever having been attached; in fact the evidence is quite the other way. In these forms the centrale may be, instead of the centro-dorsal, really the dorso-central, in which case we should get an interesting homology with the echinoids.

The association of the holothurians with the echinoids, and hence with the crinoid-echinoid stem, seems to me to be abundantly justified. The following classification of the echinoderm groups is proposed as showing the interrelations of these groups better than any of the synopses previously published.

Phylum ECHINODERMATA

I. Subphylum ECHINODERMATA HETERORADIATA.
- A. Pelmatozoa.
  - 1. Crinoidea.
  - 2. Cystidea.
  - 3. Blastoidea.
- B. Ovozoa.
  - 1. Echinoidea.
- C. Vermiformes.
  - 1. Holothuroidea (Bohadschoidea).

II. Subphylum ECHINODERMATA ASTRORADIATA.
- A. Ophiobrachiata.
  - 1. Ophiuroidea.
- B. Stellarides.
  - 1. Asteroidea.

In this table the sequence of groups must not be taken to represent a phylogenetic line; in no class of animals is a phylogenetic sequence more difficult of conception than in the echinoderms. While the heteroradiate echinoderms are, judged by ordinary standards, more perfect than the astroradiate, judged from the echinoderm point of view solely, they can not be considered so well developed as the latter.

THE EARLY BREEDING HABITS OF AMBLYSTOMA PUNCTATUM

ALBERT H. WRIGHT AND ARTHUR A. ALLEN

CORNELL UNIVERSITY

CASUAL observations made at Ithaca, during the past eight or nine years, upon the habits of *Amblystoma punctatum* have emphasized the need of an intensive study of the early breeding habits of this species, and consequently during the spring of 1908 considerable attention was given to this phase of its life history.

The best collecting ground for this species was found to be along the eastern border of the marsh at the head of Cayuga Lake where it is skirted by a state road and by the tracks of a trolley line. Here it is necessary for the salamanders from the hill, on their way to suitable breeding grounds, to cross the tracks and in so doing many are killed by the passing cars. Heretofore, it was believed that the majority came from the ravines which cut through the hill in this locality. To test this, a trap was placed at the mouth of one of the culverts under the road. The trap yielded only eight specimens during the ten days in which the species was migrating. It would, therefore, seem that the salamanders came mainly from the hill itself. For the study of spermatophores and eggs ponds on the hilltop near the university proved most fruitful. Six ponds were visited daily. In these, countless spermatophores and several hundred bunches of eggs were deposited. A chart of each pond was prepared and upon this, for future reference, the position of several areas of spermatophores and each bunch of eggs were indicated with the date of deposition.

The first appearance from hibernation for this species from 1903 to 1908 follows:

1903, March 13.	1906, March 28.
1904, April 1.	1907, March 24.
1905, April 1.	1908, March 23.

In 1908 the first appearance occurred the evening of March 23, when the maximum and minimum air temperature, were 47° and 42° F. The water temperatures of the two ponds under observation on the following morning were 42° and 48° F., respectively. On the above dates of first appearance from 1903 to 1908, the U. S. Weather Bureau Station at Ithaca obtained the following maximum and minimum air temperatures:

Year.	Max. Temp.	Min. Temp.	Year.	Max. Temp.	Min. Temp.
1903	52° F.	31° F.	1906	51° F.	32° F.
1904	55	36	1907	61	43
1905	64	37	1908	47	42

From this it is obvious that a temperature approximating 50° F. or more almost invariably caused the species to emerge.

To verify this conclusion, a careful record of the migration across the railway in 1908 was kept and a summary follows in tabular form:

Date.	Temperature.		Number Captured Alive at Night.	Number Killed by the Cars.	Total.
	Max.	Min.			
March 24.	49°	22°		1	1
March 25.	37	19			
March 26.	65	37		15	15
March 27.	63	36	9	13	22
March 28.	72	41	31	24	55
March 29.	41	30	"cold, cloudy weather with snow flurries."[1]		
March 30.	48	33			
March 31.	43	27			
April 1.	48	27	17		17
April 4.	50	18	3 (in the trap)		3
April 6.	62	40		1	1
Total,			60	54	114

In this table as in the preceding 50° F. appears the normal effective temperature of migration. The crest

[1] Climatological Report for March, 1908. New York Section of the Climatological Service of the Weather Bureau in Cooperation with Cornell University. By W. M. Wilson, p. 19.

of the migration in 1908 came when the maximum air temperature ascended to 60° or 70° F. In two other years the same conditions obtained as shown in the accompanying data:

Date of Crest.	Max. Temp.	Min. Temp.
1901, April 21.	72°	42°
1901, April 22.	86	62
1907, March 27.	70	45
1908, March 28.	72	42

The males begin the migration, as the following table will indicate:

Date (1908).	Number Killed.	Number Captured Alive.
March 26,	15 males.	
March 27,	5 males, 4 females.	6 males, 3 females.
March 28,	10 males, 14 females.	12 males, 19 females.
April 1,		7 males, 10 females.

Thus we see the males began the migration. The next evening, the females appeared in small numbers and the third evening they predominated and continued thus for the remainder of the migration.

In 1908, the migration each evening across the railway began between 7:30 and 8:00 o'clock. By means of an acetylene lamp, the salamanders were observed crawling along close to the rail, often following it for some distance. At times they were seen attempting to cross the track by raising themselves erect on their tails. Even with this aid, scarcely more than the head came above the rail. In this position they often remained until crushed by the passing cars. Generally, however, they followed along the rail until they came to the joints, where the projecting bolts enabled them to work their way over.

The evening upon which spermatophores were first deposited, two salamanders were seen "nosing" each other, and one of the two depositing spermatophores. Neither was captured, and so to determine if this were a part of the regular courtship of the species, several salamanders collected along the track were taken to the laboratory

and placed in jars as follows: Jar No. 1, seven males; No. 2, several each of males and females; No. 3, a male and a female. These specimens had not reached the water, and were carried to the laboratory in a dry bag. The temperature of the water in the jars was 65° F., or fifteen to twenty degrees warmer than that in the ponds.

The seven males of jar no. 1 showed no excitement and deposited no spermatophores until a day or two later. Then, the total of spermatophores for the whole seven was much less than that deposited by the single male of jar no. 3.

In jar no. 2 the males and females became excited the moment they were placed together and many spermatophores were deposited at once. This experiment was repeated the following evening with a different set of salamanders and the males began to deposit spermatophores within fifteen minutes after being placed with the females. No eggs were deposited earlier than two days after the deposition of the first spermatophores.

In jar no. 3 the male, at first, showed no signs of excitement, but upon coming in contact with the female, he became very restless, and "nosed" her about in a definite manner. It seemed to be the object of the male to bring the top of his head in contact with the venter of the female. The throat region of the female seemed to be preferred, although he often began in the cloacal region or even at the tip of the tail and rubbed the dorsolateral part of the head along her whole ventral side. After each performance of this kind, the male swam away and grasped one of the sticks with its hind legs, bringing the cloaca close to the stem. The tail quivered for a moment and, with an arching of the region just caudad of the cloaca, the vent was lifted from the spermatophore. Then, he immediately returned to the female and began again the "nosing" process. The time consumed in depositing a spermatophore varied from 3 to 16 seconds, the periods for thirteen consecutive depositions being: 5, 3, 6, 10, 13, 12, 7, 11, 12, 16, 11, 10, 10 seconds, re-

spectively. In this way twenty-two spermatophores were deposited in 45 minutes.

Most of this time the female remained quiet. Three times, however, she slowly moved over a spermatophore until the vent rested upon it. Then the hind limbs closed about it. In this position the female remained, each time, for ten to fifteen seconds and apparently made no effort to take any portion of the spermatophore into the cloaca as does Diemyctylus. It seemed to us rather that there was a simple passage of the spermatozoa from the spermatophore into the cloaca of the female.

Evidently, then, the female must be present at the time the spermatophores are deposited and in this we find the explanation for the delay in deposition of spermatophores after the species has first appeared from hibernation. The males begin the migration but no spermatophores are deposited until the arrival of the females. In the spring of 1908 the migration began the evening of March 26, but spermatophores were not recorded until the morning of March 28, after the arrival of the females. With the arrival of the females and the ensuing courtship, spermatophores are deposited. These are usually found in stagnant or slowly moving water, four to twelve inches deep, though they are occasionally recorded in water one and one half to two feet in depth. They occur in groups numbering from 2 to 125, covering an area of one half to three feet square. The usual number in a group is between 30 and 50. The spermatophores and the spermatozoa recently described by Smith[2] need no discussion here.

After the first spermatophores are deposited, an interval elapses before the first eggs are recorded. In former years this interval has varied from a few hours to seven days and we had been led to believe that the females did not come to the ponds until their eggs were ripe. This belief is no longer tenable. After the cloacal

[2] Smith, B. G., "The Breeding Habits of *Amblystoma punctatum* Linn.," AMERICAN NATURALIST, XLI, No. 486, June, 1907, pp. 381-385.

inclusion of the spermatozoa several hours or days may elapse before the eggs ripen and ovulation occurs. "In 1903 one interval of 2 days was recorded; in 1904, one of 4 days; in 1906, one of 6 days; in 1907, 4 days in one pond, 5 in another, and 7 in a third."

"Egg-laying generally begins about the first of April. In two or three of the last eight years, eggs have been noted before that date. In this period, the earliest record is March 20, 1903. In 1901 they did not begin depositing eggs until after the middle of April. The egg-laying for the species may extend over a month or more. Rarely do we find fresh eggs after May 1. In 1907 our latest record for fresh eggs is April 30; our latest for fresh spermatophores in the same pond, April 27."[3]

The number of eggs in a complement varies from 130 to 225. These may be deposited in one to ten bunches, two or three per female being a fair average. There is not necessarily uniformity in the size of the bunches, for one female was known to deposit two bunches, one of 140 eggs, the other of 32.

At least thirty minutes are usually consumed in depositing a normal bunch of eggs. One female in depositing a bunch of 140 eggs remained beneath the surface for over an hour. During this time she neither strove to get into a position where she could keep her nostrils out of the water, nor did she once arise to the surface for air. As in other cases, the eggs came out slowly without apparent effort or straining, sometimes but four in a minute. During deposition she was motionless, except for occasional slow movements of the tail. Immediately after deposition, however, for two or three minutes, she swayed back and forth vigorously to disengage herself, for the fresh jelly stuck to the under side of her tail and cloaca. Ten hours later another bunch of 32 eggs finished the complement.

[3] Wright, A. H., "Notes on the Breeding Habits of *Amblystoma punctatum*," *Biological Bulletin*, Vol. XIV, No. 4, April, 1908, p. 286.

NOTES AND LITERATURE

MARINE BIOLOGY

Papers from the Tortugas Laboratory of the Carnegie Institution of Washington, Vol. I, 191 pp., Vol. II, 325 pp. (Carnegie Institution of Washington Publications No. 102 and 103, 1908.)

The first collection of memoirs published in the name of the laboratory itself, from this practically tropical marine station, is highly creditable to the students who made the researches, to the director of the laboratory, Dr. A. G. Mayer, and to the great Institution which, on the financial side, has made the studies possible. Still more it is an impressive embodiment of the perception and conception that the sea is a vast, inexhaustible mine of the raw material out of which biological science is constructed; and that this material can be transformed into finished, useful product only on the ground to which it is native. Such writings drive home the truth with special force that would we really know nature we must go where nature is; we must study her *in her home.*

The two volumes contain nineteen papers written by fourteen naturalists, and the range of topics is almost as wide as the field of marine zoology. Yet nearly every one of these papers contains something, some of them many things, that a biologist who daily breathes the air of a large, expansive biological philosophy will want to make memorandum of for future use.

The apparel of the matter presented approaches, though does not reach, perfection. The most serious defect in the outer garments is the lack of aid to general consultation. Not only is there no alphabetical index, but the list of papers at the beginning of each volume is without page references, so one must hunt through the volume for any paper he may want to consult. The principle of the greatest good to the greatest number is against allowing scientific books, especially, to go out wanting such useful incidentals as these. The numberings and letterings of some of the illustrations are too small and indistinct to be easily read by artificial light.

Defects in some of the inner garments are more unfortunate than any in the outer. It is not necessary as one of the authors seems to think, to "investigate into" a subject. To just investi-

gate it is enough. "Further observations are needed . . . especially with reference as to whether," etc. Why the "as to"? This sentence is bungling. But worse than bungling is the statement that "organic data function" in controlling, etc. Such expressions as this can not be let off on the plea of hasty composition, imperfect proof reading, established usage within a special field, or something of the sort. They mean hazy thinking. Literary form is not a vital thing especially to technical science. Nevertheless, considerable attention to it pays in the long run for effort in this way is promotive of clean, clear thought.

It seems to the reviewer that the word "reaction" is being overworked by some students of animal behavior. What more is there in a medusa's "fishing reaction" than in its plain fishing? And what is the gain in speaking of a bird's alighting on a stake as a "reaction"? There is a quality seemingly possessed in some degree by all minds, that tends to accept a new name for an old familiar phenomenon as in some way more explanatory of that phenomenon than the old name. Anything that encourages this tendency is not good for objective science. More, perhaps, in science than in any other domain of knowledge is there need of vigilance against bondage to words.

The subjects treated in the collection may be ranged under these heads: *Cytology, normal development, regeneration, faunal zoology* and *animal behavior*. Some of the papers fall exclusively under one head while others contain matter belonging to two or more. Such notice and comment as can be made here will be ranged under these headings.

Cytology: H. E. Jordan ("The Germinal Spot in Echinoderm Eggs") concludes that the chromosomes in *Echinaster crassispina* are derived from the nucleolus, and that they arise inconstantly in different species of echinoderms from any part of the germinal vesicle that contains the chromatin material, such containers being either the nucleolus or nuclear reticulum or both, and that nothing in this research supports the theory of individuality of the chromosomes. The same author ("The Spermatogenesis in *Aplopus mayeri*") finds an accessory chromosome in the phasmid studied and believes the "history of this accessory chromosome gives evidence that it at least possessed a strict morphological and probably also a physiological individuality." One would like to know whether this statement implies that there might be

a morphological without a corresponding physiological individuality. If such an individuality is implied it is a queer kind of individuality, or would be for any other bodies than chromosomes. But chromosomes have had so many queer things attributed to them that queerness with them has almost ceased to be queer.

In a third paper ("The Relation of the Nucleolus to the Chromosomes in the primary Oöcyte of *Asterias forbsii*") the same author expresses the belief that "all the hereditary elements are persistently held by the chromosomes . . . and that these merely receive nutritive material from the nucleolus." It may be granted that the figures and descriptions presented show material to be transferred from the nucleolus to the chromosomes. What the evidence is that this material is all nutritive and none of it hereditary would be extremely important. Certainly no such evidence is presented in this paper.

The fourth paper that contains cytological matter is "The Habits and Early Development of *Linerges mercurius*," by E. G. Conklin. The egg of this medusa presents concentric layers, the outermost of which is protoplasm nearly free from yolk. As in the eggs of various other cœlenterates, cell-division, at least the first division, begins in this peripheral layer; but contrary to what has been held for some other species, the nuclei and chromosomes are here somewhat distant from the point at which the first visible changes toward division occur. There seems, consequently, no observational ground for supposing that this outer layer does not actually start up the division. This would appear to be a very significant point. Conklin gets no evidence that cell-division is ever amitotic in this species as it has been reported to be in one or two other cœlenterates.

Normal Development: W. K. Brooks and B. McGlone show ("The Origin of the Lung of Ampullaria") that in the pulmonate studied, the lung seems to be quite a different structure from that of other pulmonates and hence the conclusion is reached that "there is no reason to think that there is any ancestral connection or relation between the lung of Ampullaria and that of the pulminates." In the paper by Conklin noted under cytology, it is shown that gastrulation in the medusa studied usually takes place by invagination, but sometimes by the immigration of a mass of endoderm cells at the vegetal pole, and the author remarks on the close relationship between the

two processes. The off-hand way in which this fact is now treated, as compared with the almost frantic contention of twenty years ago that the two are fundamentally different, at least in phylogenetic significance, may well be reflected upon when our minds are turned toward theoretical biology.

Regeneration: Under this head there are two valuable papers. One ("An Experimental Study of the Rate of Regeneration in *Cassiopea xamachana*") is by Chas. R. Stockard, and the other ("Some Internal Factors concerned with the Regeneration of the Chelæ of the Gulf-weed Crab") is by Chas. Zeleny. Stockard finds no support in this research for the hypothesis that activity of the regenerating part accelerates or influences in any special way the regeneration. By cutting pieces of various shapes and sizes from the bell of the medusa, he gets the interesting result that on the animal itself the "*regeneration rate is fastest from the portion from which most tissue has been removed*"; and on the pieces cut away regeneration is "*fastest from the part from which the least tissue has been removed.*" The reviewer would raise the inquiry, Does not this conclusion say essentially that the *removed tissues of Cassiopea are replaced in the way necessary to effect the quickest and surest restoration of the original form of the animal regardless of the form and place of the cut?*

Zeleny's researches were directed at two fundamental points: "The quantitative determination (1) of the effect of successive removal of an organ upon its power to regenerate and (2) of the character of the changes, if any, produced in the uninjured parts of the animal by such removal." The summarized results are: (1) "When the correction for change in power of regeneration with size or age is made it is found that successive removal neither retards nor accelerates the regeneration of the right chela." The criticism may be ventured that this conclusion is too unqualified for the number of tests made, there having been but three removals of the same chela in the same individual. As we commit ourselves more and more to quantitative methods in biology, we shall see more and more clearly, so it appears, the importance of the principle of "large numbers." On the second object of the research the result was: "The removal and regeneration of the right chela produces no change in the growth of the uninjured left chela."

Faunal Zoology: The titles belonging primarily under this head are: "The Pelagic Tunicata of the Gulf Stream," by W.

K. Brooks; "Notes on the Medusæ of the Western Atlantic," by H. F. Perkins; "Helminth Fauna of the Dry Tortugas," by Edward Linton; "A Variety of Anisonema vitrea," by C. H. Edmondson.

A sad interest attaches to the paper by Professor Brooks, it having been published after its author's death. Fitting indeed it is that some of the last works from Brooks's masterly hand should be on the group of animals on which his most distinguished observational researches were made. A few unimportant inadvertencies occur in the paper due to the fact that illness prevented the author from putting his manuscript in final form for publication. Some of the figures of Plate I are labeled *S. florida*, and some *S. floridana*. *Floridana* is the right name. The title is somewhat misleading since no general treatment of the tunicate fauna of the Gulf Stream is contained in the paper. As a matter of fact "observations on certain morphological points in the subgenus Cyclosalpa" would have been a better title for the first and second parts of the paper. Perhaps the most important general point discussed by Professor Brooks is that of the similarity between the muscle bands of Salpa and Doliolum. He had previously tried to dispel the erroneous distinction, as he believed, between the two that is suggested by the terms Hemimyaria as applied to Salpa, and Cyclomyaria as applied to Doliolum.

In a third section of the paper written in collaboration with Carl Kellner, a new appendicularian, *Oekopleura tortugensis*, is described. Some "Notes on Embryology" add a little to our meager knowledge of the development of this group of animals.

Perkins's paper on Medusæ is by no means a faunistic study in the narrow sense, it containing quite as much that would come under the head of animal behavior as under that of faunal zoology. One of the new species, *Cladonema mayeri*, is treated at length, not only the hydroid, and medusa forms being fully described, but as well various activities and attitudes being dwelt upon in a lively, appreciative manner. There may be a little danger in speaking of a jelly-fish as "evincing the keenest interest in the prospect of a meal," but such expression has at least the merit of recognizing the coordinated though complex and characterizing activities of the organism under a special stimulus; and at the present time the tendency is to allow lower organisms too little rather than too much of psychic life.

Efforts to secure embryos of *Cassiopea xamachana* were unavailing, no males being found even though over one hundred individuals were examined!

Linton's studies on parasitic worms lead him to the conclusion that generally these organisms are not as abundant either in species or individuals, for an equal number of hosts (fishes) in tropical as in northern waters.

An interesting case of identification is mentioned by Linton. The spiral valve of some shark, with its contents, came to him for study. From the entozoa present, taken with the other intestinal contents, he concluded that the organ belonged to *Galeocerdo tigrinus*. It was later found that the jaws of the specimen had been saved. Examination of these proved the original identification to have been right. Question: Where were the "determinants" of the characters by which this identification was made? Were they in the germ-cells of the shark or in those of the entozoa that inhabited the shark's intestine? Of course the case would present no difficulty to a consistent determinantist because the determinant doctrine is founded (unwittingly) exactly on such an *a priori* basis that observed facts can not touch it. As well expect to hurt a ghost with a charge of buck shot, as the determinant theory with objective facts.

Several new species and genera of endoparasitic worms are described in the paper.

Animal Behavior: Under this head come the largest number of titles and, on the whole, probably the most important observations contained in the volumes. This is as it should be, coming, as the studies do, from a laboratory located by design in a peculiarly rich zoological region that is at the same time remote from the great centers of scientific activity. The titles are: "The Annual Breeding-Swarm of the Atlantic Palolo," by A. G. Mayer; "Rhythmical Pulsation in Seyphomedusæ," by A. G. Mayer; "Habits, Reactions and Associations in *Ocypoda arenaria*," by R. P. Cowles; "Habits, Reactions and Mating Instincts of the Walking Stick, *Aplopus mayeri*," by C. R. Stockard; "A Contribution to the Life-History of the Booby and Man-o'-War Bird," by F. M. Chapman; "The Behavior of Noddy and Sooty Terns," by J. B. Watson; and "An Experimental Field-study of Warning Coloration in Coral-reef Fishes," by Jacob Reighard.

As already indicated, some of the papers noticed under other

heads contain interesting matter that belongs here. This is especially true of Conklin's paper on Linerges. It is practically out of the question to give within the limits of a brief review an adequate summary of the contents of this group of papers. The Atlantic Palolo has been under observation by Dr. Mayer for nine years, and various interesting details in the "swarming" of this species have been made out. Besides the principal swarm (near the last quarter of the moon, between June 29 and July 28) there may be a few smaller swarms before and after this. Experiments indicate that moonlight falling on the rocks in which the worms live is indispensable to the swarming.

Mayer's studies on the pulsation of the medusa of *Cassiopea xamachana* is a continuation of work of his previously reported one. The idea that sea water is a balanced solution for this species, and that the animal manufactures its own stimulant to the rhythmical contractions by the "constant formation of sodium oxalate in the terminal entodermal cells of the marginal sense-organs," is still further dwelt upon. Mayer concludes, in agreement with some other observers working on other animals, that in this species, "*conductivity* of the subumbrella tissue is *independent* of *contractility*. Dr. Cowles's article on the "sand-crab" is especially distinguished at first sight by some of the admirable illustrations it contains. It is shown that this crab, in which one chela is decidedly larger than the other, almost always digs its burrow with the side having the smaller chela and enters the burrow after it is dug, with that side in the lead. This, Dr. Cowles remarks, is probably advantageous to the animal in that the larger chela is in the more favorable position for defense. It would seem that this case might have an interesting bearing on the question whether structures take their characteristic forms to meet demands imposed upon them or are used to the best advantage for the organism after they are in existence. In which service are the chela exercised more, in digging or defending and capturing? Possibly the question might be answered observationally. The investigator concludes that the crabs do not distinguish colors visually and do not hear in the ordinary sense; that they see outlines; that the so-called auditory organs are equiliberating organs; that the tactile sense is well developed; and that the animals have memory and profit by experience, and form habits.

The peculiar structure and habits of the walking-stick,

Aplopus, afford the animals protection in a high degree according to Stockard's investigations. Under certain circumstances when the antennæ are removed the "forelegs are readily pressed into service as feelers." Males were found to copulate even in a dark room with the amputated abdomina of the females.

Chapman gives some interesting information on the domestic and civil polity of the booby and the man-o'-war bird. For example, the male and female booby seem to change off in their home duties, the one staying with the nest for a time while the other fishes. Each pair of birds is closely limited to its own small nest area during the breeding time, the rule being enforced by prompt action on the part of members of the colony generally if a particular individual ventures outside his own precincts. The booby seems to have the habit of laying two eggs, only one of which yields a bird. Although not belonging properly under the present heading, mention may be made of Chapman's observation on the order in which the feathers of pterylæ appear and the rate at which they grow. This seems to the reviewer an important subject and one deserving more attention than it has received.

Without minimizing the value of the papers so far noticed, the two still unnoticed, namely those of Watson and Reighard, are probably the most valuable of the whole collection, judged by the number and character of the observations recorded. In his introductory remarks Professor Watson refers to his work as preliminary and speaks with some doubt about the possibility of its being continued. From the beginnings made on several problems of the utmost interest, it is greatly to be hoped that the Tortugas Laboratory will see to it as one of its first concerns that these investigations are kept up. To get some clear light on the one problem of how terns which seemingly have never been over the ground before, can find their way from Cape Hatteras to the Bird Key, something like a thousand miles, would amply justify the expenditure of the institution's entire income for a number of years were so heavy an outlay necessary. Fortunately the work would probably not be greatly expensive. Biologists will do well to recognize that exactly in such phenomena as these occultism and superstition have their strongest roots to-day, and that these roots are by no means frail and sickly. Any victory that science can win in these frontier regions counts for more toward the general enlightenment of

mankind than many won in already well cultivated conquered territory. For the many facts brought out on the relation of the sexes during the breeding period; on the care of progeny; on the instincts and habits of the young; on the intelligence, individual and comparative, of the two species studied; and many other topics, the paper itself must be consulted.

Reighard's investigation being in a field that has long been a storm-center of theoretical biology, will probably attract more readers than any other one in the volumes. In the reviewer's opinion it will, too, exercise a wide and beneficent influence toward rectifying one of the most remarkable aberrations to which scientific speculation has been subject in any domain of science for many a decade. It was the reviewer's privilege a few years ago to spend some time observing the fishes about the coral-reefs of the Hawaiian Islands. From this experience as well as from various others more or less kindred, he is convinced of the essential soundness of Reighard's results. More than that, he is convinced that any naturalist, the windows of whose mind are not darkened with the heaviest screens of adverse dogma, would be likewise convinced were he to examine the evidence for himself.

We must be content with a single quotation from this paper:

Coral-reef fishes are not conspicuous because they are in the reefs; they are in the reefs because they are conspicuous and can not therefore leave the reefs, and because, being in the reefs and taking food as they do, there is no reason for their being inconspicuous. The reefs condition their conspicuousness; they are in no sense its cause.

We should certainly want more light than the author has given on the meaning of the statement that reefs condition but in no sense cause the conspicuousness of the fish. But passing this as of minor importance it is to the first part of the statement that we turn for the real meat of the case. If it be really true, and we recognize the truth, that the color of these fishes has arisen we know not how, but that having become thus elaborate and conspicuous, the fishes find protection as well as food among the corals, then are we at the threshold of the problem of how the color has arisen, with our senses and wits open to receive evidence of whatever sort bearing on the problem. The unfortunate thing about the natural selection theory has been not so much the error it contains as the fact that it has been made an *absolutist theory*: one of the sort, that is, that *shuts the*

door in the face of inductive science. It is time to be undeceived in this matter.

Wm. E. RITTER.

LA JOLLA, CALIF.,
Sept. 20, 1909.

EXPERIMENTAL ZOOLOGY

Inheritance of Color in Pigeons.—The breeding experiments of pigeons, described by R. Staples-Brown in the *Proceedings of the Zoological Society of London* for 1908, pages 67–104, are of interest because he repeated certain experiments by which Darwin obtained a reversionary type resembling *Columba livia.* Darwin concluded that domesticated pigeons sprang therefore from the wild rock pigeon. The varieties of pigeons used by Staples-Brown were with one exception identical with those used by Darwin and the experiments were planned on similar lines. Darwin's experiment, it will be recalled, was as follows:[1] A black Barb was crossed with a white Fantail and a black Barb with a red Spot (white bird with tail and tail coverts red having a red spot on the forehead). Upon mating hybrids produced by these two crosses Darwin obtained a pigeon identical with *Columba livia,* excepting that "the head was tinted with a shade of red, evidently derived from the Spot, and was a paler blue than in the rock pigeon." Staples-Brown substituted a black and white Nun for Darwin's red Spot which was not readily obtainable.

A Nun is a white bird with certain well-defined markings of black, blue, red or yellow. The individuals used in Staples-Brown experiments were black and white, the black appearing on the chin and throat, part of the outer flight feathers, a few secondaries and tertiaries, the tail and upper and under tail coverts. The Barb pigeon is self-colored, black, red, yellow, dun or white, with a small beak and the skin around the eyes broad and carunculated. Black Barbs only were used in these experiments. The Fantails used were white. When the Barb × Fantail hybrids were bred to the Barb × Nun hybrids no reversionary types were produced. These experiments were discontinued owing to lack of space. However, when Barb × Fantail hybrids were mated together some of the offspring had blue feathers. The blue color was chiefly on the tail as described by

[1] "Animals and Plants under Domestication," 2d edition, Vol. I, p. 209.

Darwin. A black tail bar was present and the wing coverts and back were of a smoky black color, obscuring the wing bars which are common to the rock pigeon. The reversionary type in some cases appeared in the F_1 generation. A similar result was obtained by Darwin in the F_1 generation from a Nun and a red Tumbler.

The author explains the fact of the reversionary blue not appearing until the F_2 generation in the Barb $\times$ Fantail cross, by assuming that the F_1 individuals contain some element which prevents the appearance of blue. This, he holds, is the factor for black self color, which is epistatic to blue. In the recombination of factors in F_2, those combinations containing blue without the black factor produce individuals with blue feathers, while those with the black factor exhibit black feathers but no blue ones.

Reference is made to other cases of reversion (sweet Peas and Stocks) in which its occurrence is due to the meeting of complimentary factors. He adds, "In the case of the Barb $\times$ Fantail cross the evidence is not yet sufficient to show whether the factors needed to produce the atavistic condition are all present in the Barb and their effect merely hidden by the presence of the black factor, or whether a necessary factor is introduced by the fantail; but the fact that no blues came in the F_2 made from an F_1 (Barb $\times$ Fantail) $\times$ F_1 (Barb $\times$ Nun) distinctly suggests that some factor of the blue did come from the Fantail."

The general result of the Barb $\times$ Fantail experiments shows a dominance of black and blue to white. This dominance, however, is imperfect, as the majority show some white feathers. In the F_2 generation from such crosses, the following types were obtained:

Black.
Black with some white feathers.
Blue.
Blue with some white feathers.
Red.
White with some colored feathers.
White.

The significance of the presence or absence of the white feathers is obscure. It was first thought that the white feathers indicated that the bird was producing white-bearing gametes. This is not true in all cases.

In matings of blues with white feathers, whites were produced, and a definite proportion of homozygous blues was to be expected. With one exception, however, all the blues produced from these matings showed some white feathers.

Some of these were probably homozygous, but it could not be tested without making use of a large number of such birds. The order of dominance was found to be black, blue, red and white. In minor characters, such as irides, color of beak and claws, the author obtained the following results; white irides dominate black, and there is some evidence of correlation between white iris and black plumage. There was also marked correlation observed between the pigment in the beak and to some extent in the claws, and the plumage. In general, white-plumage birds have white beaks and claws. In the case of eye-wattles, red is dominant over flesh color.

B. B. HORTON.

The Study of
Stellar Evolution

An Account of Some Modern Methods of
Astrophysical Research

By GEORGE ELLERY HALE

The introduction of photographic methods, the improvement of telescopes, and the rapidly increasing appreciation of the value to astronomy of physical instruments and processes, have revolutionized the observatory. From a simple observing station it has been transformed into a great physical laboratory, where images of the sun and stars are studied with many powerful instruments, and celestial phenomena are experimentally imitated with the aid of electric furnaces and other sources of intense heat. The result has been a great gain in our knowledge of the origin, development, and decay of stars. This book explains in a popular way how the life histories of the sun and stars are investigated. One hundred and four half-tone plates, made from the best astronomical negatives, place before the reader the most recent results of celestial photography in most of its phases.

250 pages, 104 plates, 8vo, cloth, net $4.00, postpaid $4.27.

METHODS IN PLANT HISTOLOGY

By CHARLES J. CHAMBERLAIN, Ph.D.

of the Department of Botany in the University of Chicago

Second Edition, Illustrated.

AN INDISPENSABLE BOOK FOR STUDENTS OF BOTANY

THIS BOOK contains directions for collecting and preparing plant material for microscopic investigation. It is based upon a course in botanical micro-technique and is the first complete manual to be published on this subject. It aims to meet the requirements, not only of the student who has the assistance of an instructor in a fully equipped laboratory, but also of the student who must work by himself and with limited apparatus. Freehand sectioning, the paraffin method, the celloidin method, and the glycerine method are treated in considerable detail. In later chapters specific directions are given for making such preparations as are needed by those who wish to study the plant kingdom from the algae up to the flowering plants. Formulas are given for the reagents commonly used in the histological laboratory.

The new edition includes a description of Klebs's methods for securing reproductive phases in the algae and fungi, and chapters on the Venetian turpentine method, microchemical tests, free-hand sections, special methods, and the use of the microscope. The volume is thus enlarged from 168 to 272 pages.

$2.25 net; $2.39 postpaid.

ANIMAL MICROLOGY

PRACTICAL EXERCISES IN MICROSCOPICAL METHODS

By MICHAEL F. GUYER

An indispensable book for teacher, physician, student, or novice who wishes to learn how to prepare his own material for microscopical examination. There are special chapters on the preparation and examination of embryological material, blood, bacteria, and objects of general interest, and on the collection and preparation of material for the microscopical work in a course in elementary zoology. In an appendix nearly three hundred tissues and organs with directions for properly preparing them for microscopical study are tabulated. Sufficient account of the theoretical side of microscopy is given to enable the student to get satisfactory results from his microscope.

250 pp., 8vo; net $1.75, postpaid $1.88

Address Dept. 62

The University of Chicago Press, Chicago and New York

The American Naturalist

A Monthly Journal, established in 1867, Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Organic Evolution and Heredity

CONTENTS OF THE MAY NUMBER

The Categories of Variation. Professor S. J. HOLMES.

The General Entomological Ecology of the Indian Corn Plant. S. A. FORBES.

Notes and Literature: *Biometrics*—Some Recent Studies on Growth. DR. RAYMOND PEARL. *Experimental Zoology*—Cuénot on the Honey Bee, Professor T. H. MORGAN. *The Upholding of Darwin*—Poulton and Plate on Evolution, V. L. K.

CONTENTS OF THE JUNE NUMBER

Heredity and Variation in the Simplest Organisms. Professor H. S. JENNINGS.

The Color Sense of the Honey Bee — Is Conspicuousness an Advantage to Flowers? JOHN H. LOVELL.

Variation in the Number of Seeds per Pod in the Broom, Cytisus scoparius. Doctor J. ARTHUR HARRIS.

Present Problems in Plant Ecology:

The Trend of Ecological Philosophy. Professor HENRY C. COWLES.

The Present Problems of Physiological Plant Ecology. DR. BURTON LIVINGSTON.

Notes and Literature: Notes on Evolution, V. L. K. DeVries's Species and Varieties, DR. GEORGE H. SHULL. *Embryology* — On the Totipotence of the First Two Blastomeres of the Frog's Egg. DR. J. F. MCCLENDON.

CONTENTS OF THE JULY NUMBER

Selection Index Numbers and their Use in Breeding. DR. RAYMOND PEARL and FRANK M. SURFACE.

A Contribution to the Theory of Orthogenesis. Dr. ALEXANDER G. RUTHVEN.

The "Presence and Absence" Hypothesis. Dr. GEORGE HARRISON SHULL.

Present Problems in Plant Ecology: Vegetation and Altitude. Professor CHARLES H. SHAW.

Shorter Articles and Correspondence: Pleistocene Swamp Deposits in Virginia. Dr. EDWARD W. BERRY.

Notes and Literature: *Heredity*—A Case of Non-Mendelian Heredity. Dr. W. J. SPILLMAN.

CONTENTS OF THE AUGUST NUMBER

The New Flora of Krakatau. Professor DOUGLAS HOUGHTON CAMPBELL.

A Male Crayfish with Some Female Organs. Professor E. A. ANDREWS.

Present Problems in Plant Ecology:

Problems of Local Distribution on Arid Regions. Professor VOLNEY M. SPAULDING.

The Relation of the Climatic Factors to Vegetation. Professor EDGAR N. TRANSEAU.

Notes and Literature: Recent Experiments on the Inheritance of Coat Colors in Mice, Professor T. H. MORGAN. Some Experiments in Breeding Slugs. Professor T. D. A. COCKERELL.

CONTENTS OF SEPTEMBER NUMBER

On an Early Tertiary Land-connection between North and South America. Dr. R. F. SCHARF.

Notes on the Relations of the Molluscan Fauna of the Peruvian Zoological Province. Dr. WILLIAM HEALEY DALL.

Remarkable Development of Starfishes on the Northwest American Coast; Hybridism; Multiplicity of Rays; Teratology; Problems in Evolution; Geographical Distribution: Professor A. E. VERRILL.

Shorter Articles and Correspondence: Is there a Selective Elimination of Ovaries in the Fruiting of the Leguminosæ: Dr. R. HARRIS.

Notes and Literature: *Ichthyology*—Ichthyological Notes, President DAVID STARR JORDAN. *Parasitology* — Professor H. B. WARD. *Plant Cytology*—The Permanence of Chromosomes in Plant Cells, Dr. BRADLEY M. DAVIS.

CONTENTS OF THE OCTOBER NUMBER

The Non-muscular Articulations of Crinoida. AUSTIN HOBART CLARK.

On Some Dinichthyid Armor Plates from the Marcellus Shale. BURNETT SMITH.

Are Species Realities or Concepts only. Professor J. H. POWERS.

Shorter Articles and Discussion: A Light Weight, Portable Outfit for the Study and Transportation of Ants. EDITH N. BUCKINGHAM. Comparison of Cænolestes with Polyprotodonta and Diprotodonta. PAULINE H. DEDERER.

Notes and Literature: *Comparative Psycholoy* — Bohn's "The Birth of Intelligence": Professor H. S. JENNINGS. *Mammalogy*—Osgood's Revision of the Mice of the Genus Peromyscus, Dr. J. A. ALLEN, LEO ERRARA, Professor CHARLES E. BESSEY.

Single Number 35 Cents **Yearly Subscription, $4.00**

The NATURALIST will be sent to new subscribers for four months for One Dollar

THE SCIENCE PRESS

Garrison, N. Y. **Sub-Station 84: NEW YORK** **Lancaster, Pa.**

VOL. XLIII, NO. 516 DECEMBER, 1909

THE AMERICAN NATURALIST

A MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

CONTENTS

Page

I. The Cuticula and Subcuticula of the Trematodes and Cestodes. Professor HENRY S. PRATT. 705

II. The American Toad (Bufo lentiginosus americanus, LeConte). NEWTON MILLER. 730

III. Observations on Copulation among Crawfishes, with Special Reference to Sex Recognition. Dr. A. S. PEARSE. 746

IV. Shorter Articles and Correspondence: Degeneration accompanying Imbreeding. Professor C. B. DAVENPORT. A Note on the Prairie-dog Owl which Resembles the Rattlesnake's Rattle: Dr. J. ARTHUR HARRIS. 754

V. Notes and Literature: The Causation of Sex, Professor H. E. JORDAN. . . 756

VI. Index to Volume XLIII. 763

THE SCIENCE PRESS

LANCASTER, PA. GARRISON, N. Y.

NEW YORK: SUB-STATION 84

The American Naturalist

MSS. intended for publication and books, etc., intended for review should be sent to the Editor of THE AMERICAN NATURALIST, Garrison-on-Hudson, New York.

Articles containing research work bearing on the problems of organic evolution are especially welcome, and will be given preference in publication.

One hundred reprints of contributions are supplied to authors free of charge. Further reprints will be supplied at cost.

Subscriptions and advertisements should be sent to the publishers. The subscription price is four dollars a year. Foreign postage is fifty cents and Canadian postage twenty-five cents additional. The charge for single copies is thirty-five cents. The advertising rates are Four Dollars for a page.

THE SCIENCE PRESS

Lancaster, Pa. Garrison, N. Y.

NEW YORK: Sub-Station 84

Entered as second-class matter, April 2, 1908, at the Post Office at Lancaster, Pa., under the Act of Congress of March 3, 1879.

TO ORNITHOLOGISTS AND MUSEUMS

W. F. H. ROSENBERG

Importer of Exotic Zoological Specimens

57 Haverstock Hill, N.W., England

Begs to announce the publication of a new Price List (No. 11) of **Bird Skins**. This catalogue contains over 5,000 species, and is the largest and most complete price list of birds ever published. It is arranged in systematic order, based on the classification of the British Museum "Catalogue of Birds," with authors' names, indications of localities, and an index to families. It will be sent gratis and post free on application, as will the following lists:

No. 7, Mammals; No. 8, Birds' Eggs;
No. 9, Reptiles, Amphibia, and Fishes.

Largest stock in the world of specimens in all branches of Zoology.

Specimens sent on approval.

Fifty Years of Darwinism

Comprising the eleven addresses in honor of Charles Darwin delivered before the American Association for the Advancement of Science.

8vo, 274 pp. $2.00, net.

CONTENTS: Introduction, T. C. Chamberlin, Walker Museum; Fifty Years of Darwinism, Edward B. Poulton, Oxford University; The Theory of Natural Selection from the Standpoint of Botany, John M. Coulter, University of Chicago; Isolation as a Factor in Organic Evolution, David Starr Jordan, Stanford University; The Cell in Relation to Heredity and Evolution, Edmund B. Wilson, Columbia University; The Direct Influence of Environment, Dr. D. T. MacDougal, Carnegie Institution of Washington; The Behavior of Unit-Characters in Heredity, W. E. Castle, Harvard University; Mutation, Chas. B. Davenport, Station for Experimental Evolution, Cold Spring Harbor; Adaptation, Carl H. Eigenmann, Indiana University; Darwin and Paleontology, Henry Fairfield Osborn, Columbia University; Evolution and Psychology, G. Stanley Hall, Clark University.

Henry Holt & Company

34 West 33d St., New York
378 Wabash Ave., Chicago

THE
AMERICAN NATURALIST

VOL. XLIII *December, 1909* No. 516

THE CUTICULA AND SUBCUTICULA OF TREMATODES AND CESTODES

PROFESSOR HENRY S. PRATT

HAVERFORD COLLEGE

THE membrane which forms the outer covering of the body of trematodes and cestodes and is usually called the cuticula differs in certain important particulars from that of other invertebrates, and its morphological significance has long been a matter of dispute. The most noticeable feature of this difference is the apparent lack of a hypodermis in these worms, the cuticula being bounded on its inner surface by the superficial muscle layers and the parenchyma which fills the body-cavity.

In the last few years, however, a theory of the cuticula, which in the early years of modern helminthology was the prevailing one, has been revived by Professor F. Blochmann (1896), who has presented its claims to recognition with so much force and ability that it has been accepted by most helminthologists and zoologists as best accounting for the facts. It has also found its way into some of the best text-books and bids fair to become, in the ordinary course of events, one of the dogmas of science.

According to this theory, the cuticula of trematodes and cestodes is a true cuticula morphologically, which is secreted by a hypodermis, as in other invertebrates. This hypodermis, however, has undergone a metamorphosis, for instead of forming a continuous layer of cells situated

immediately beneath the cuticula, it has dropped back of some or all of the superficial muscle layers into the parenchyma, its constituent cells have become more or less separated from one another, and it forms the broken or irregular tissue called the subcuticula.

Fig. 1, which is taken from Blochmann's paper and ap-

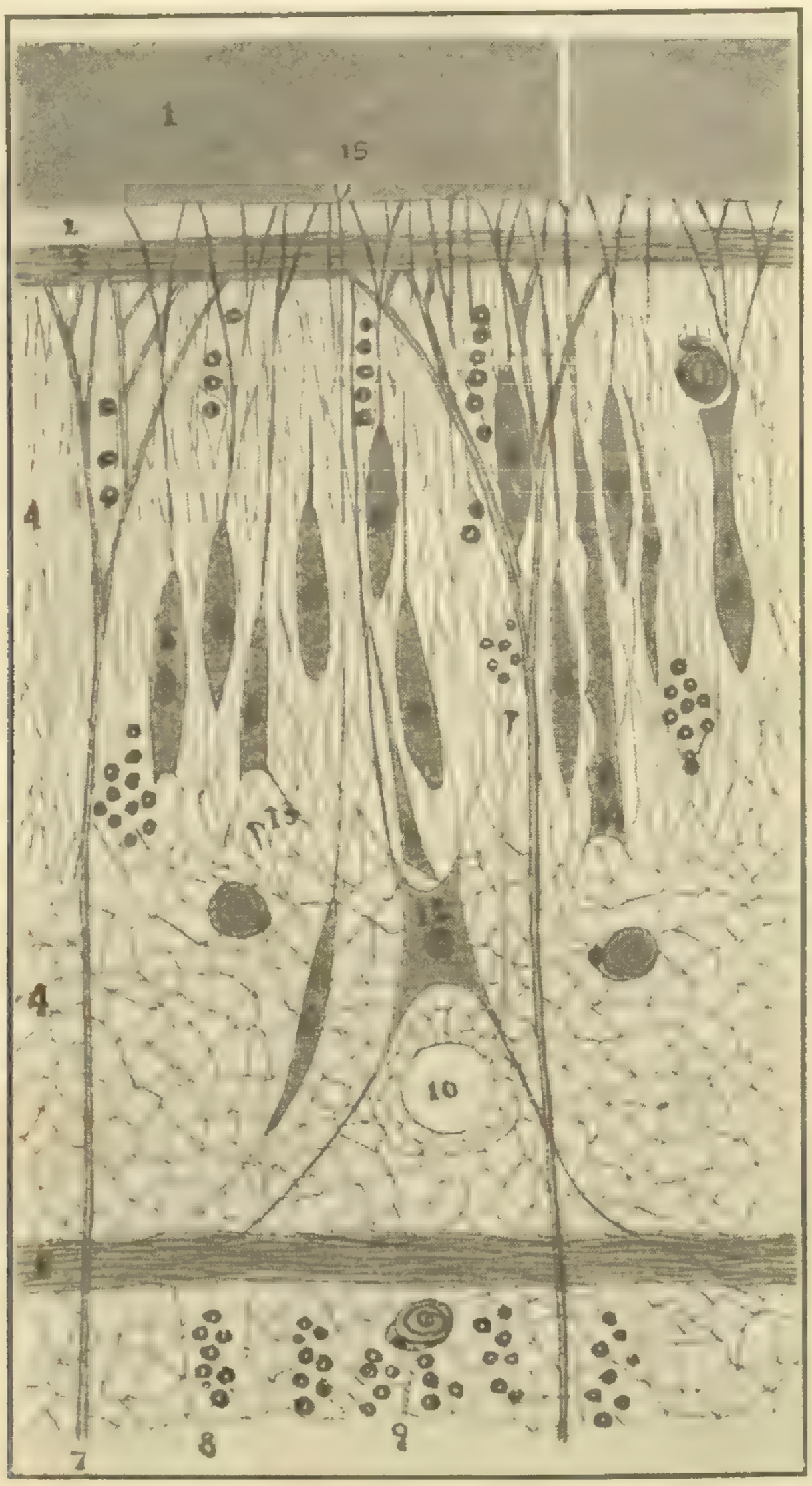


FIG. 1. Transverse section from Ligula, a cestode (after Blochmann). 1, cuticula; 2, basal membrane; 3, circular muscles; 4, parenchyma; 5, subcuticular cells; 6, nerve; 7, dorsoventral muscles; 8, longitudinal muscles; 9, calcareous body; 10, excretory canal; 11, sense-cell; 12, myoblast; 13, flame-cell; 14, gland-cell; 15, sense-organ.

pears also in Claus and Grobben's "Lehrbuch," Braun's "Menschliche Parasiten" and Lankester's "Zoology," represents a section of the body-wall of a cestode (Ligula) and shows the relation of the cuticula to the subcuticular

cells as conceived by Blochmann and adopted by the authors of these text-books.

Fig. 2 from Hein (1904), who follows Blochmann closely, shows the same relations in the digenetic trematodes. It will be seen in both these figures that the subcuticular cells form a distinct although irregular layer and are joined with the inner surface of the cuticula by long projections. These Blochmann and Hein regard as the ducts through which formative material is added to

FIG. 2. Longitudinal section from *Fasciola hepatica*, a digenetic trematode (after Hein). 1, cuticula; 2, spine; 3, circular muscles; 4, longitudinal muscles; 5, oblique muscles; 6, subcuticular cells; 7, parenchyma.

the cuticula, of which these cells are thus the matrix. It will further be noticed in these figures that the subcuticular cells apparently do not form a part of the parenchyma in which they lie, and also that among them are sense cells and gland cells which are usually conceded to have an epithelial origin.

Another theory of the cuticula which is not very different from Blochmann's is that of Brandes (1892), who also considers the structure in question to be the product of the subcuticular cells (Fig. 3). These, however, he conceives to be single-celled glands which are joined with

the cuticula by means of ducts passing between the superficial muscle fibers. Brandes's theory is based upon an examination of a considerable number of monogenetic and digenetic trematodes, in both of which groups he finds practically identical structural conditions in the cuticular and subcuticular layers. His drawings, however, are very diagrammatic. The subcuticular cells certainly do not exist in any trematodes in the form in which he shows them, and those in his figures of monogenetic trematodes are not the subcuticular cells at all, but the single-celled glands which are present at the forward end of most of these worms.

FIG. 3. Transverse section from *Onchocotyle appendiculata*, a monogenetic trematode (after Brandes). 1, cuticula; 2, parenchyma; 3, circular muscles; 4, longitudinal muscles; 5, subcuticular cells; 6, oblique muscles.

Tennent (1906) and others have adopted Brandes's view. It will at once be noted that the main difference between his theory and that of Blochmann lies in their interpretation of the subcuticular cells, the former holding them to constitute a hypodermis and to be consequently an epithelium of ectodermic origin, the latter considering them simple gland cells which are derivatives of the parenchyma.

These important theories, although they may seem to account for the facts in the animals investigated and to place the whole matter upon a substantial logical basis, have, however, met with considerable opposition, and, it seems to me, are not well grounded. It is quite evident that if they are true they must have universal application. If the subcuticular cells are the matrix of the cuticula, whether we consider them to be single-celled glands or the constituent parts of a hypodermis, then they must be present in all trematodes and cestodes, since this peculiar cuticula characterizes all of these worms (with the

exception of the Temnocephalidæ) from their early larval stages to those of the adult.

But this is far from being the case. The subcuticular cells are wanting in probably the whole group of monogenetic trematodes, also in most of the Aspidobothridæ and in certain other digenetic trematodes. Goto (1894, 1899) has made a careful anatomical study of over forty species of monogenetic trematodes belonging to some sixteen genera, and has found no subcuticular cells in any

FIG. 4. Transverse section from *Dionchus agassizi*, a monogenetic trematode (after Goto). 1, cuticula; 2, parenchyma; 3, muscles; 4, single-celled glands; 5, parenchyma nuclei.

of them (Fig. 4). He directed his attention specially to the discovery of these cells in the worms studied by Brandes, but says:

> Although I directed my special attention to the point, I have utterly failed to observe those subcuticular cells so beautifully drawn by Brandes in his figures in the very same genera that he describes.

Cerfontaine (1899) has also made a study of some twenty-eight species of monogenetic trematodes with the same result (Fig. 5).

It is true that peripheral single-celled glands are present in probably all of these worms, the ducts of which can be easily seen (Figs. 1 and 4) to pass not merely to but through the cuticula to the outside surface of the body. These gland cells are usually grouped at the forward end

of the body or in the neighborhood of the suckers, and are variously interpreted as sticky or mucous glands or as irritants to increase the flow of the juices which serve as the food of the worm. They do not extend over the whole body or any large part of it, and are not the subcuticular

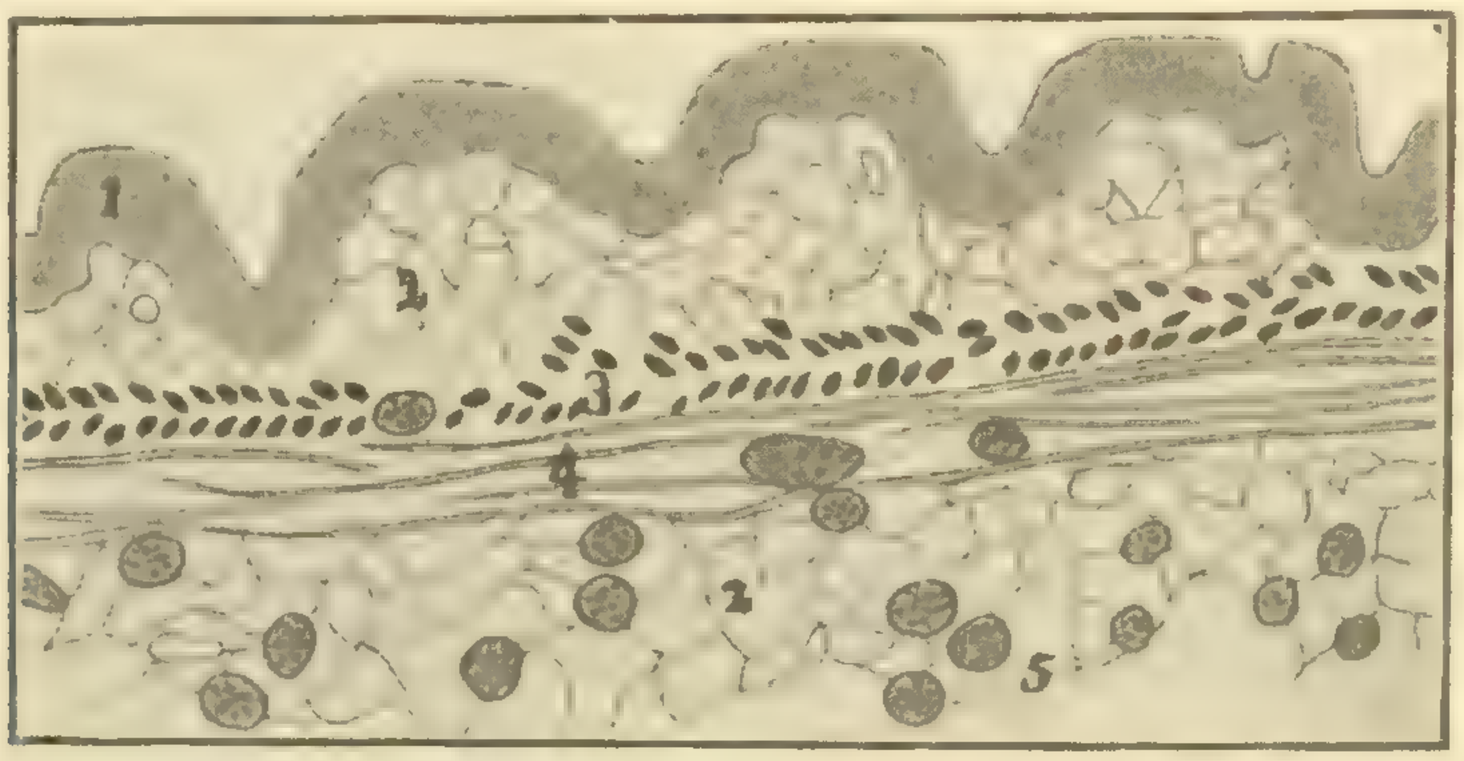


FIG. 5. Longitudinal section from *Squalonchocotyle vulgaris*, a monogenetic trematode (after Cerfontaine). 1, cuticula; 2, parenchyma; 3, circular muscles; 4, longitudinal muscles; 5, parenchyma nuclei.

cells, nor are they so considered by any authors who have studied them. They also differ markedly in shape from the subcuticular cells, being more or less pear-shaped and regular in outline, each cell having a distinct and single

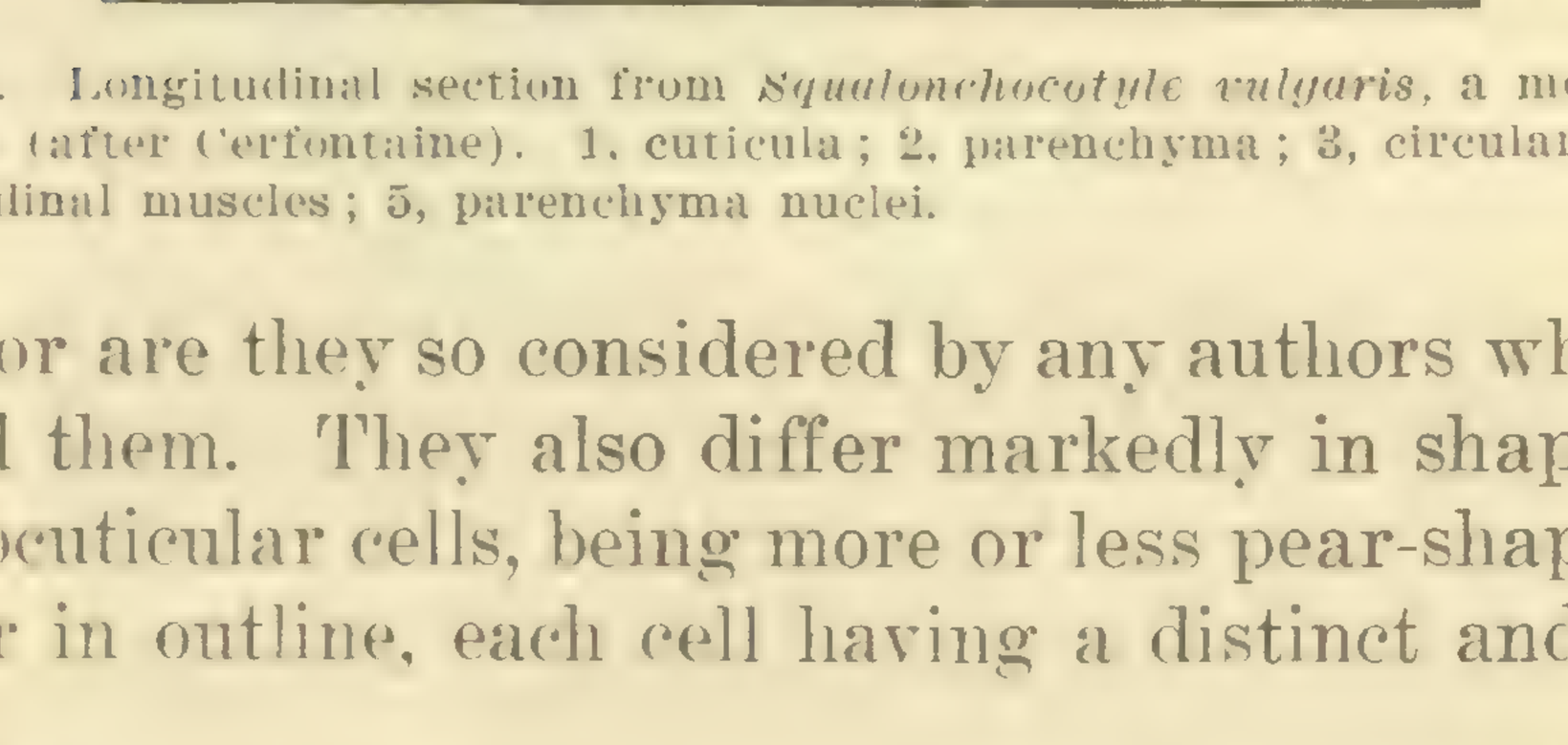


FIG. 6. Longitudinal section from *Stichocotyle nephropis*, an aspidobothrid (after Nickerson). 1, cuticula; 2, muscles; 3, parenchyma; 4, intestine; 5, pharynx; 6, mouth; 7, parenchyma nuclei.

duct of large size. The subcuticular cells, on the other hand, are often irregular in shape, often anastomosing with one another and in many cases having the appearance of parenchyma cells. They also show no ducts at all,

but in many forms are connected with the cuticula by branched or anastomosing processes (Figs. 1 and 2) which are interpreted by many to be ducts.

The lack of subcuticular cells in Aspidobothridæ has been shown by Monticelli (1892) and Nickerson (1902) for Cotylogaster, Nickerson (1894) for Stichocotyle (Fig. 6), and Osborn (1904) for Cotylaspis. Single-celled glands are, however, present in all these worms.

In the other digenetic trematodes and in cestodes, also, although subcuticular cells have been shown to be present in most of the forms whose finer structure is known, it is certain that some do not possess them. In *Distomum palliatum* and *Distomum reticulatum*, for instance, Looss (1885) found none of them, and in *Hemiurus crenatus* and *Gasterostomum gracilescens* Lander (1904) and Tennent (1906), respectively, found them only in very small numbers. In all digenetic trematodes and cestodes, also, it can very often be shown that the cells in question bear no adequate relation to the cuticula beneath which they lie. Thus they are present sometimes in certain parts of the body only, as has been shown in my study of Apoblema (1898), in which the appendix of the youthful distome, although covered with exactly the same cuticula as in the rest of the body, is entirely without subcuticular cells. The suckers, also, in cestodes and the tail of the cercaria have none of these cells, although they possess a cuticula.

In many digenetic trematodes, too, the subcuticular cells, although present, are entirely too few in number to produce the thick cuticula present, as shown in *Hemiurus crenatus* (Fig. 7) by Lander, and in numerous other cases. It must be remembered in this connection that the cuticula of trematodes and cestodes is probably at all times a growing tissue, which is constantly being renewed on its inner surface in proportion as it wears away on its outer, so that if the subcuticular cells are its matrix they should be equally present in all parts of the body and at all times of the animal's active life.

In many digenetic trematodes the cuticula is not of equal thickness on all parts of the body and these variations in thickness are not correlated with corresponding differences in the subcuticular cells beneath them. For instance, the cuticula of the appendiculate distomes has numerous transverse rings which give a longitudinal section a serrated appearance. These rings are due solely to

FIG. 7. Transverse section from *Hemiurus crenatus*, an appendiculate distome (after Lander). 1, cuticula; 2, longitudinal muscles; 3, subcuticular cells; 4, parenchyma.

variations in the thickness of the cuticula, the inner surface of it being quite smooth, and we might expect the subcuticular cells, if they secreted the cuticular, to be larger or more numerous beneath the rings. This is, however, not the case, these cells showing no variations whatever beneath these cuticular rings.

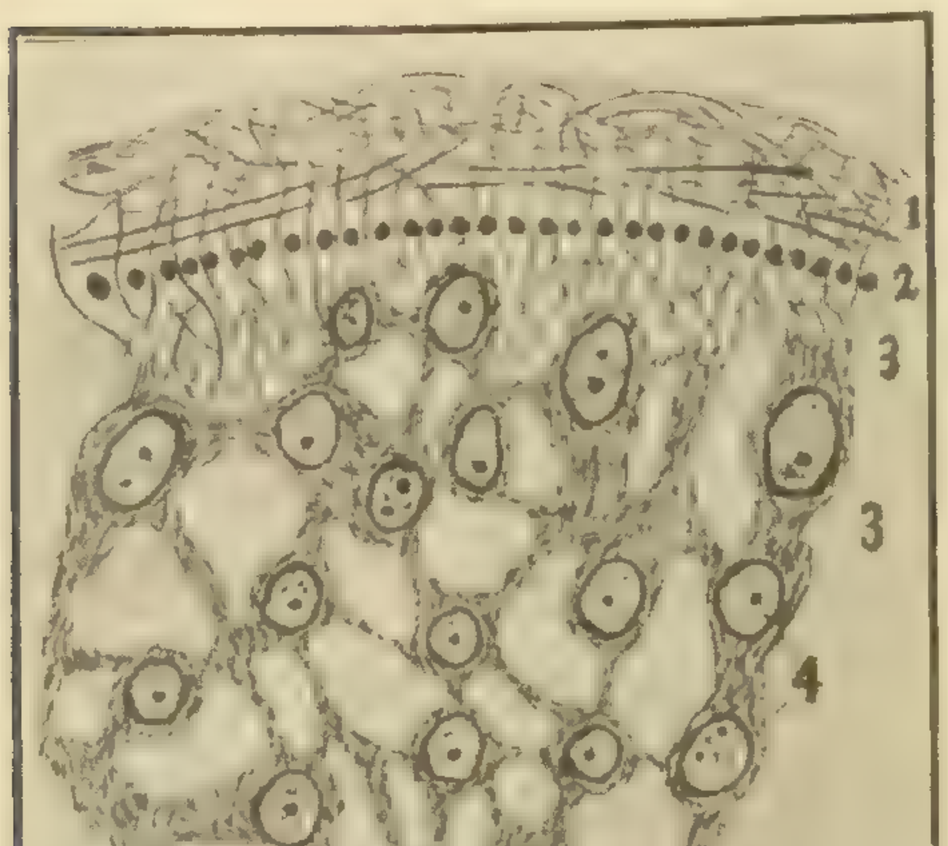
The relations of the spines, hooks, scales and other special cuticular structures to the subcuticular cells also furnish an argument against the epithelial or glandular nature of the latter. These spines and hooks are of very common occurrence and are often very prominent objects in trematodes and cestodes, their function usually being to aid in anchoring the parasite to its host. They are seen in their simplest form in the digenetic trematodes, (Fig. 2) in which they usually appear as specialized parts of the cuticula. In the monogenetic trematodes and the cestodes, on the other hand, they are often of huge size and of more or less complex structure and may extend beneath the cuticula among the muscles and the parenchyma cells.

That these organs are similar in essential structure and

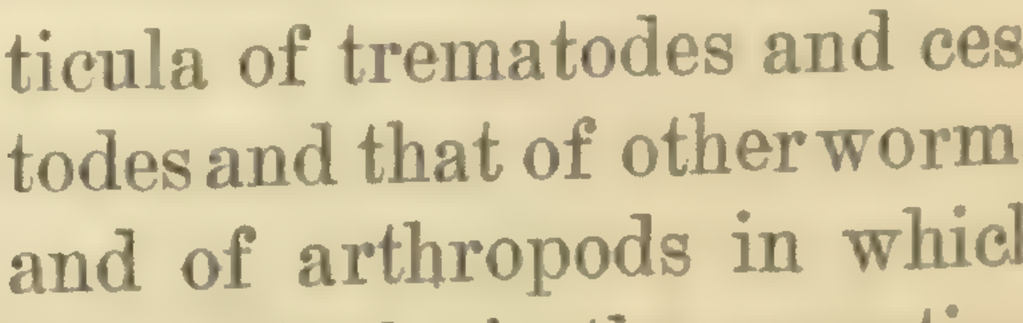
in origin to the cuticula has been very well shown by Looss (1894), Young (1908) and other authors, who have traced their development and growth.

If now the cuticula is the product of the underlying subcuticular cells, we should expect to find some special development of them beneath the hooks and spines, especially where these are very large, just as in the integument of insects a cuticular hair or scale is invariably situated over the enlarged hypodermal cell which produces it. Nothing of the sort exists, however, in trematodes and cestodes. The subcuticular cells beneath the hooks and spines do not differ in size, number or arrangement from the adjacent cells, and in the monogenetic trematodes, which are often provided with gigantic hooks, no subcuticular cells at all are present. In the six-hooked embryo of cestodes the hooks make their appearance in the embryonic parenchyma, while there are as yet no subcuticular cells present. The parenchyma is thus the matrix of the hooks at this early stage of the animal's existence.

Another point of importance is the essential difference in structure between the cuticula of trematodes and cestodes and that of other worms and of arthropods in which the cuticula is the secretion of an undoubted hypodermis. In the former the characteristic lamellate structure of a



8



9

FIG. 8. Section of wall of young cysticercus of *Tænia serrata* (after Young). 1, cuticula; 2, muscles; 3, parenchyma; 4, parenchyma nuclei.

FIG. 9. Section of body wall of *Squalonchocotyle vulgaris*, a monogenetic trematode (after Cerfontaine). 1, cuticula; 2, nuclei in the cuticula; 3, parenchyma; 4, muscles.

typical arthropod or worm cuticula is never present (although it may be made up of several layers), but, on the other hand, a fundamentally fibrous structure can often be demonstrated with perfect clearness, the fibers being sometimes in very evident connection with the parenchyma beneath and a portion of it (Figs. 8 and 9).

In fact, the so-called ducts of the subcuticular cells are nothing more nor less than the fibrous projections of these cells which, together with similar projections of the parenchyma cells themselves, sometimes extend to, and occasionally, especially in young animals, into the cuticula. In certain cases these fibers may arrange themselves so as to form a series of vertical strands in the cuticula, passing between its inner and outer surfaces, and have been interpreted in the past to be pore-canals, structures which are probably not present in any trematodes or cestodes. Whatever toughness of texture the cuticula of these worms possesses is probably due to this fundamentally fibrous or leathery structure. The cuticula is further exceedingly elastic; it is often very soft or even semi-fluid and easily destroyed in caustic potash and as the result of maceration; and it is never moulted as a whole nor can it be usually separated from the tissues beneath—all of which characteristics are foreign to the cuticula of other worms and of arthropods.

The differences between an undoubted hypodermis and the subcuticular cells are also fundamental and very striking, and are not satisfactorily explained by Blochmann, who compares with them the hypodermal cells of Hirudo and other animals which may be more or less separated from one another by parenchyma and other tissues. The origin of these cells forms the embryonic parenchyma, as shown clearly by many authors, and the frequent anastomosing of them with one another and with the surrounding parenchyma, are characters which no hypodermis possesses.

It is true that there is a strong superficial resemblance between the subcuticular cells in cestodes—but seldom or

never in trematodes—and epithelial cells, without which it is not likely that any one would ever have thought of this epithelial theory. These cells in cestodes are, as we have seen, usually elongated and spindle-shaped and lie parallel to one another, so that they look a good deal like isolated epithelial cells. But it must also be noticed (Fig. 1) that all the other cellular elements of the peripheral region—the parenchyma cells, the gland cells and the sense cells—are also elongated and spindle-shaped and lie parallel to one another and to the subcuticular cells. Ap-

FIG. 10. Golgi section from a cestode (Ligula) showing the branched insertion of the dorsoventral muscles in the cuticula (after Zernecke). 1, cuticula; 2, the muscles; 3, sense-organ; 4, nerves; 5, sense-cell.

parently some common cause, in the nature of a tension in a dorsoventral direction, has acted upon the entire peripheral region of the body of the worm, distorting more or less all the structures in it. Leuckart (1886) has suggested—and Leuckart's suggestions are always fruitful—that this spindle form is due to the action of the powerful dorsoventral muscles which run across the

proglottid and are inserted in the cuticula of each surface by numerous branching strands (Fig. 10). He even thought that the spindle cells might be the tendons of these muscles, which, however, is not the case, since Zernicke (1895) and others have demonstrated the branched insertions just mentioned. It is my opinion, however, that it is the pull of these muscles and especially of their branched insertions which interweave themselves among all the peripheral tissues of the body (Fig. 10), which has thus distorted all the cellular elements in this region and caused them to assume their characteristic shape and appearance. And this opinion is confirmed by the fact that in the scolex and between the proglottids, where these muscles are weak or absent, the subcuticular cells are not spindle-shaped, but have the form of ordinary parenchyma cells (Leuckart).

The embryological and larval history of these worms also furnishes arguments against the epithelial theory. The cuticula comes into existence, both in trematodes and cestodes, before the subcuticular cells have differentiated and grows independently of them (Figs. 8 and 11). Its early growth has been well described by Looss for trematodes in Diplodiscus (1892) and in a considerable number of distomes (1894) and by Roewer (1906) in distomes, and for cestodes by Young (1908) in *Cysticercus pisiformis*. These authors show also very conclusively that when the subcuticular cells do finally make their appearance it is as differentiations of the embryonic parenchyma cells and that at no time is anything like an epithelium present in the position in which they are found (Fig. 8).

The moulting of the outer epithelium (ectoderm) in larval trematodes and cestodes has also an important bearing upon this question, inasmuch as in consequence of it the adult worm is entirely composed of tissues derived primarily from the interior embryonic cell mass (endoderm or mesenchyme). The subcuticular cells can not consequently be of ectodermal origin and can not be

homologous to the hypodermis of other invertebrates. In trematodes this moulting may occur in each of the larval stages. It has been directly observed in the miracidium many times, among others by both Thomas (1883) and Leuckart (1886) who saw the miracidium of *Fasciola hepatica* shed its ciliated ectoderm when it entered the liver of *Lymnæa trunculata*. In the redia and cercaria stages it has also been directly observed by a number of investigators. Looss has made the most complete record of his observations. He (1892, 1893, 1894, also Braun, 1893, p. 818) has seen both the redia and cercaria shed its outer epithelium in about a dozen species of distomes, as just remarked, after which procedure the young worm was covered with the definitive cuticula. This Looss considers the product of secretions of the entire body of the parenchyma.

Although the cercaria has thus been seen to shed its peripheral epithelium, there have been recorded a number of cases where it is not shed all at one time, portions remaining until the cercaria is fully grown or nearly so. The appendiculate distome I described some time ago (1898) was a good example of this procedure. The appendix of the young worm in this case retained its cercarian ectoderm although the male genital organs were mature and spermatozoa were being produced. The remainder of the body was without an epithelium, but was covered by the characteristic cuticula, which was also present beneath the epithelium on the appendix. This epithelium was soon after moulted and then the outer covering of the appendix was exactly similar to that of the rest of the body.

In cestodes the early stages of development are very similar to those of trematodes, the ectoderm having been observed by Schauinsland (1885), Leuckart (1886) and others to be moulted in exactly the same way. It is the opinion of many students of cestodes, however, that the stage in which an outer epithelium is present is passed over in most of these animals. The young worms thus

never have an outer epithelium, but the characteristic cuticula is their earliest body-covering.

Although there can be no doubt that the outer epithelium of trematode and cestode embryos and larvæ is often, perhaps usually, moulted, it must be mentioned that cases have also been recorded in which no such moulting has apparently taken place. Schauinsland (1883) has shown that in the embryo of *Distomum tereticolle*, the ectoderm gradually loses its cell boundaries and nuclei and becomes metamorphosed into a cuticula. A similar process has been described by Leuckart (1886) in the young redia of *Fasciola hepatica*, by Zeller (1872) in the embryo of Polystoma, and by other authors.

FIG. 11. Section of wall of a young cysticercus of *Tænia serrata* (after Young). 1, cuticula; 2, parenchyma.

These facts and others which will be mentioned have led many helminthologists to subscribe to a third theory of the cuticula of trematodes and cestodes—that which sees in it a metamorphosed or cuticularized epithelium (ectoderm). This is one of the oldest of the theories relating to the cuticula, having been first proposed by Wagener in 1855, and in later years having such able supporters as Monticelli, Goto, Nickerson and Braun, although the last named has apparently abandoned it in favor of Blochmann's theory. It is based mainly upon the facts that embryonic and larval ectoderms have been observed in a degenerate condition as just stated, and also that frequently nuclei are found imbedded in the adult cuticula. These nuclei are sometimes well formed (Fig. 12), but often have the appearance of being in a more or less broken-down condition and to be degenerating. Open spaces and vesicles are also often present in the cuticula.

Much has been observed which supports this theory. Braun (1893, p. 590) found numerous oval nuclei in the cuticula of *Monostomum mutabile*, Maclaren (1905) found

them in Distomum sp. (Fig. 12), Monticelli (1892, 1894) in a number of trematodes, Nickerson (1902) in Cotylogaster, Cerfontaine (1899) in *Squalonchocotyle vulgaris* (Fig. 9): many other authors also have seen and described them. There can be no doubt that however one may interpret the alleged cuticularization of the embryonic and larval ectoderms,—and Brandes, Looss, Braun and others will not admit that it has been demonstrated,

FIG. 12. Section of the cuticula of a distome containing nuclei (after Maclaren). 1, cuticula; 2, nucleus imbedded in cuticula.

—nuclei or nuclei-like bodies occasionally appear in the cuticula of both larval and adult trematodes and cestodes. These have been variously interpreted by different authors. Blochmann (1896), for instance, asserts that they are the end organs of sense cells which are imbedded in the cuticula, while Looss (1893) thinks they may be portions of formed material in the act of passing from the parenchyma into the cuticula.

It seems to me that the occurrence of nuclei in the cuticula has been recorded by too many competent observers to be explained away in any such manner. They undoubtedly do occasionally occur, being either nuclei which are parts of a degenerating epithelium or perhaps those which belong to the peripheral portion of the parenchyma and have become enclosed in the rapidly forming and growing cuticula. This last probability is strengthened by the observation of Maclaren (1905) and others that such nuclei occur most frequently in the cuticula of young worms, and by those of Young (1908) and Cerfontaine (1899) who show, respectively, that the cuticula

of the very young larva is composed essentially of fibers and nuclei closely bound together (Fig. 11) and that the adult cuticula may be in direct connection with the subjacent parenchyma and contain some of its nuclei (Fig. 9). It is conceivable, however, notwithstanding these facts, that foreign objects such as particles of coagulated blood, which often adheres to the outer surface of these worms, could be forced into the soft cuticula from the outside as a result of the pressure to which the worms are often subjected in their natural environment, or perhaps in the compressor or under the cover-glass of the investigator, and thus appear like degenerating nuclei in it. The vesicles, which often appear in the cuticle, are probably artefacts due to the influence of reagents on the soft cuticula of a dying or a compressed animal. The cuticula also macerates very rapidly, in fact it is often the first part of the body to show death-changes, and may easily become vesicular by the passage of fluids or gases into it from the parenchyma or from the outside.

In my own opinion this theory of the metamorphosed epithelium breaks down, at least as a universal theory, for several reasons. In the first place, the outer epithelium is undoubtedly moulted in very many larval trematodes, as has been observed by many competent observers, and a worm can not both shed its epithelium and still enjoy the possession of it, even in a modified form. The theory can not thus have general application. In the second place, even if the ectoderm of the embryo or larva is cuticularized in certain cases, as has been observed, the cuticula of the adult worm is not yet accounted for, as the worm increases in size many-fold, often many thousand-fold, while growing from the larval to the adult condition. In other words, the cuticula of the mature worm may be quite a different structure from that of the larva, and if it is true that the cuticula of the larva is a metamorphosed epithelium, then that of the adult is formed of a different material and in a different way. Inasmuch as the cuticula is constantly growing on its inner

surface and being flaked off on its outer, it is not a structure which is formed once for all but one which depends on a more or less uniform secretion from the tissues beneath.

What then is the morphological significance of the cuticula of trematodes and cestodes if it is neither a metamorphosed epithelium nor the product of an underlying hypodermis or of single-celled glands. I believe that it is the peripheral portion of the parenchyma which forms the outer coating of the body after the disappearance of the larval epithelium (ectoderm), and which has been solidified into a thick membrane by the secretion of cuticular substance from the whole body of the parenchyma. That the entire parenchyma can thus have a secretory function is proved by the formation by it of the fluid with which it is permeated and its vesicles are filled and also of that which fills the cavity of a cysticercus.

This theory seems to have originated with Leuckart (1886, p. 367). It has been explained and defended at great length by Looss (1893, 1894, also Braun 1893, p. 818, note) and subscribed to by Pratt (1898), Cerfontaine (1899) and Young (1908). It is in certain respects an unusual theory, inasmuch as it implies the absence of an integumental covering of ectodermic origin, which is characteristic of the rest of the Metazoa. But the life conditions of trematodes and cestodes are peculiar and unusual. These worms are exclusively parasitic animals, being the only large groups of Metazoa, so far as I recall, of which this is the case, and this parasitic habit is undoubtedly correlated with the disappearance of the larval ectoderm and the formation of the parenchymatous cuticula, as well as other special features of the structure of these worms.

The most primitive trematodes, the Temnocephalidæ, are an exception to the rest of the group in possessing an integument composed of a cuticula with an underlying hypodermis, although having the typical trematode structure in other respects. These animals are found adhering

to the surface of turtles and fresh-water crustaceans and are not true parasites, inasmuch as they feed upon small animals in the water and not upon the vital juices of the host. They probably form a connecting link between turbellarians and trematodes, representing the first step of the ancestors of the latter towards the acquisition of parasitic habits. The next step was taken as the result of the migration of the worms from the surface into the mouth and cloaca and on to the gills, and then into the internal organs, of the aquatic hosts. The worms thus became true parasites. They learned to feed upon the blood or the other juices of the host and were habitually enclosed or immersed in its tissues and exposed to the disintegrating action of its fluids. It is probable, as a result of these things, that the changes occurred which characterize the body-covering of these worms. The integument which is common to most worms apparently would not furnish a sufficient protection to animals thus situated, and it consequently came about in the course of their evolution that the outer epithelium with its cuticula was moulted or at least disappeared and the parenchyma acquired the property of forming a thick cuticula-like membrane on its outer surface to protect the animals from the peculiar dangers of their environment. A protective function similar to this is, as Leuckart points out, very frequently exercised by cuticula-like connective tissue structures of various kinds throughout the animal kingdom.

Von Graff (1903) has made the observation, it is interesting to note, that in certain of the parasitic turbellarians (Syncelidium) a process similar to this has evidently gone on, for the animals have lost their integumental epithelium together with its cilia and are covered with a cuticula similar to that of trematodes.

The first steps in the formation of the cuticula have been minutely observed, as already stated, in the trematodes by Looss (1892, 1903) and Roewer (1906) and in cestodes by Young (1908). According to Looss, it first

appears as a fine line between the muscle-layers and the outer epithelium (ectoderm) of the redia and cercaria, which gradually broadens and when the epithelium is finally shed, becomes the outer covering of the body. Looss has observed this proceeding in a dozen or more different species of trematodes and believes it to be general to the entire group.

According to Young, the cuticula of the young cysticercus is a delicate layer which is composed of a groundwork formed of fibrillar projections of the embryonic parenchyma cells and a homogeneous translucent cement-like substance produced by these cells (Figs. 8 and 11). The subcuticular cells have not yet differentiated from the embryonic parenchyma. The young cuticula soon begin to scale off on the outer surface and is constantly being added to on the inner. In the course of time two layers show themselves in the cuticula, the inner of which alone contains the cement-like substance, the outer layer, which in later stages may be very thin or be entirely lost, forming the so-called hair-layer which sometimes characterizes the outer surface of cestodes and is exclusively fibrillar.

The later history of the cuticula is a continuation of its larval history. Although formed principally as a secretion of the parenchyma, it is at all times a part of it and will often show, even in the adult stage, a fundamentally fibrillar structure. It is also, as has been stated, never moulted and can not be easily separated from the structures beneath.

Very important in a study of the whole question, is the relation of the gonoducts and the excretory vesicle to the surrounding parenchyma, inasmuch as the walls of these structures have essentially the same structure as the outer body-wall, being lined by a cuticula at the back of which are the parenchyma and usually muscle fibers. What then is the developmental history of these ducts? It has recently been shown by Balss (1908) in cestodes and Roewer (1906) in trematodes that the history of the

formation of the gonoducts as well as their structure, is essentially similar to that of the body-wall. The walls of each of these ducts (except those of the uterus in cestodes) are formed at first of a single-layered epithelium which develops from a primitive chord of epithelial cells by the appearance in it of a lumen. This epithelium, however, quickly degenerates and disappears and at the same time the surrounding parenchyma secretes a cuticula which forms the permanent coating of the tubes. The spines which are often present in the cirrus and vagina are formed in the same way.

The terminal excretory vesicle has also primitively an epithelial wall like that of the gonoducts, as has been shown by Looss (1894) and in my study of Apoblema (1898), which is replaced by a parenchymatous cuticula as in the case of the gonoducts.

The cause of the change in the structure of the walls of these ducts from an epithelium to a parenchymatous cuticula is probably identical with that which has been brought about a similar change in the structure of the body-wall. Not only is the outer covering of the animal apt to be affected injuriously by the juices of the host, but the walls of the large ducts opening to the outside as well, and both have consequently undergone an identical transformation.

What then are the origin and function of the subcuticular cells? That they belong genetically to the parenchyma has been proved with the utmost conclusiveness by the embryological researches of Looss, Young, Balss and others. The conclusion, based by Blochmann and Hein upon anatomical evidence, that they form an epithelium needs, but has not yet received, embryological support; in fact, not a scintilla of embryological evidence has been produced either by them or any one else in the thirteen years which have elapsed since Blochmann's paper was published. And purely anatomical evidence in an obscure matter like this should be received with the greatest caution, especially since the extreme parasitism of these

worms has affected all their organs and tissues in so marked a degree.

The function of these cells is a much more difficult matter to determine, and two diametrically opposed classes of views have been expressed concerning it. According to one of these, they form a specialized tissue with either a secretory or an absorptive function. According to the other, they are an unspecialized embryonic tissue, which has no direct physiological relation to the other structures of the body.

If the almost unanimous decision of all the investigators who have studied trematodes and cestodes is to be accepted, the subcuticular cells are glandular or secretory in function and, as we have seen, the cuticula is the product of their secretion. Some years ago (1898) I suggested that they (as well as the single-celled glands) may secrete, not the cuticula itself, but some substance which tends to render the cuticula immune to the disintegrating effects of the body-fluids of the host in which they pass their lives. That the cuticula of endoparasitic trematodes and of cestodes does possess some special means of protecting itself and the other tissues of the worms seems certain. Looss, for instance, has taken *Distomum tereticolle* from the stomach of the pike, where the worm was pressed tightly against the stomach-wall by large masses of actively digesting food. Something in this case must have prevented the worm from being digested, too. This special means of defense is not to be looked for in the physical structure of the cuticula itself, which is usually soft and easily injured, but in some chemical substance which neutralizes the action of the juices of the host. It is possible that the subcuticular cells secrete some such substance, especially as the ectoparasitic trematodes, which are in most cases either not surrounded by the tissues of the host or are only partially so, do not, as we have seen, possess these cells.

What the reaction of these secretions would be must depend upon the nature of the fluid in which the worm is

immersed. If it lives in the stomach of the host, for instance, the reaction would probably be alkaline and the action of the digestive juices would thus be neutralized. In other locations the reaction would be different and might be very complex.

A small minority of investigators, however, but important and influential though small, does not believe in the glandular function of the subcuticular cells. Rindfleisch and Leuckart (1886, p. 366) first expressed the opinion that, in cestodes at least, they are simply peculiarly formed connective tissue cells which in certain places may lose their spindle form and assume quite the form of ordinary parenchyma cells. This is the case, for instance, as already stated, in the scolex and between the proglottids.

Looss (1893) also regards the subcuticular cells as connective tissue structures, interpreting them as embryonic and unspecialized cells which are destined to develop into parenchyma and muscle strands as the worm increases in size, and he supports his views with such a mass of detailed observations and such cogent reasoning that it is likely they would be generally adopted if the belief in the secretory nature of the subcuticular cells were not so firmly fixed in the literature of the times.

Looss shows that the interior cells of the germ-balls of the cercaria develop into the nervous system, the genital organs, the intestinal cœca and the parenchyma—all after the first appearance of the cuticula. But all of these cells do not at once so develop. The young worm must grow often many thousandfold before it reaches adult size, and this increase in size is made possible through the persistence in an undifferentiated condition of certain of these interior embryonic cells, which during the life and growth of the worm are constantly forming new parenchyma cells, as well as other structures. The formed parenchyma cells do not divide. In the cercarian tail, which is destined to have but a very short existence, all of these cellular elements become parenchyma cells and

muscle strands and no embryonic cells persist; hence no subcuticular cells are present.

Originally these indifferent cells lie around all of the growing organs, especially the genital organs, as well as near the periphery of the body. But in the course of the growth of the worm all disappear except those near the periphery, which become the subcuticular cells and may remain throughout life, giving rise to new parenchyma cells, and also to muscle strands and to flame-cells. In old digenetic trematodes, however, they may also disappear (Lander, Maclaren). Looss compares these cells to the cambium of plants, which is also an indifferent tissue which gives rise to certain specialized tissues throughout the life of the plant.

The only authors who have fully subscribed to this theory, so far as I know, are Nickerson (1894) and Stafford (1896), who support it by observations drawn from the study of Sichocotyle and Aspidogaster, respectively, although Schuberg (1894), Lander (1904), Balss (1908), Young (1908) and others have declared in favor of the parenchymatous origin of the subcuticular cells.

That so few have done so is probably due, as I have already indicated, to the fact that the belief in the glandular nature of the cells in question is so firmly fixed in the minds of helminthologists as to have axiomatic force. But it must never be forgotten, notwithstanding this circumstance, that this particular function has never been proven for these cells. No one has yet seen them produce a secretion and the supposed ducts that are seen in connection with them in some, although by no means in all species, and the possession of which is perhaps the principal proof which has been brought of their glandular nature, are not ducts at all. In contrast to them we might indeed place the single-celled glands, whose ducts are always perfectly plain and whose secretion can be seen. It must also be remembered that neither Leuckart nor Looss, each of whom, it will be generally conceded, has surpassed all contemporary investigators in his knowl-

edge of parasitic worms, has attributed a glandular function to these cells, but, as we have seen, has interpreted them in quite a different way.

SUMMARY

1. The cuticula of trematodes and cestodes is not homologous to that of other worms and of arthropods.

2. The cuticula of trematodes and cestodes is the peripheral portion of the parenchyma, being composed mainly of secretions of it.

3. The subcuticula is not an epithelium or a hypodermis, but belongs genetically to the parenchyma.

4. The subcuticular cells are not present in the monogenetic trematodes, in most of the Aspidobothridæ and in many digenetic trematodes, or in any trematodes or cestodes during the earliest larval stages when the cuticula first forms.

5. The function of these cells is not known, and although most authors have ascribed a glandular or secretory function to them it seems likely that they form an indifferent, embryonic tissue which develops into specialized tissues as the worm increases in size.

LITERATURE

Balss, H. H. Ueber die Entwicklung der Geschlectsgänge bei Cestoden nebst Bemerkungen zur Ectodermfrage. *Zeitschr. f. wiss. Zool.*, Bd. 91, p. 266, 1908.

Blochmann, F. Die Epithelfrage bei Cestoden und Trematoden. Hamburg, 1896.

Brandes, G. Zum feineren Bau der Trematoden. *Zeitschr. f. wiss. Zool.*, Bd. 53, p. 558, 1892.

Braun, M. Trematodes. Bronn's Klassen u. Ordn., Bd. 4, p. 306, 1893.

Cerfontaine, P. Contribution à l'Étudé des Octocotylidés. *Arch. d. Biol.*, T. 16, p. 345, 1899.

Goto, S. Studies on the Ectoparasitic Trematodes of Japan. *Jour. Coll. Sci. Imp. Univ. Jap.*, Vol. 8, p. 1, 1894.

Goto, S. Notes on some Exotic Species of Ectoparasitic Trematodes. *Jour. Coll. Sci. Imp. Univ. Jap.*, Vol. 12, p. 263, 1899.

v. Graff, L. Die Turbellarien als Parasiten und Wirte. Festschrift für 1902. Graz, 1903.

Lander, C. H. The Anatomy of Hemiurus crenatus (Rud.) Lühe, an appendiculate Trematode. *Bull. Mus. Comp. Zool.*, Vol. 45, p. 1, 1904.

Leuckart, R. Die Parasiten des Menschen, etc. 2te Aufl. Leipzig, 1886.
Looss, A. Ueber Amphistomum subclavatum, Rud. und seine Entwicklung. **Festschrift f. R. Leuckart. Leipzig, p. 147, 1892.**
Looss, A. Zur Frage nach der Natur des Körperparenchyma, etc. *Verh. Sächs. Ges. Wiss. math.-phys. Cl.,* Bd. 45, p. 10, 1893.
Looss, A. Die Distomen unserer Fische und Frösche. *Bibl. Zool.,* Heft. 16, p. 1, 1894.
Maclaren, N. Ueber die Haut der Trematoden. *Zool. Anz.,* Bd. 26, p. 516, 1903.
Monticelli, F. S. Cotylogaster michaelis, etc. Leuckart's Festschrift, p. 168, 1892.
Monticelli, F. S. Studii sui Trematodi endoparassiti. *Zool. Jahrb. Anat.,* Bd. 3, Suppl., 1893.
Nickerson, W. S. On Stichocotyle nephropis, etc. *Zool. Jahrb. Anat.,* Bd. 5, p. 447; 1894.
Nickerson, W. S. Cotylogaster occidentalis, etc. *Zool. Jahrb. Anat.,* Bd. 15, p. 597, 1902.
Osborn, H. L. On the Habits and Structure of Cotylaspis insignis Leidy. *Zool. Jahrb. Anat.,* Bd. 21, p. 201, 1904.
Pratt, H. S. A Contribution to the Life-history and Anatomy of the Appendiculate Distomes. *Zool. Jahrb. Anat.,* Bd. 11, p. 351, 1898.
Roewer, C. F. Beiträge zur Histogenese von Cercariaeum helicis. *Jen. Zeitschr. f. Naturwiss.,* Bd. 41, p. 1885, 1906.
Schauinsland, H. Beiträge zur Kenntniss der Embryonalen Entwicklung der Distomeen. *Jen. Zeitschr. f. Naturwiss.,* Bd. 16, p. 465, 1883.
Schauinsland, H. Die embryonale Entwicklung der Bothriocephalen. *Jen. Zeitschr. f. Naturwiss.,* Bd. 19, 1886.
Schuberg, A. Zur Histologie der Trematoden. *Arb. a. d. Zool.-zoot. Inst. Wurz.,* Bd. 10, p. 167, 1894.
Stafford, J. Anatomical Structure of Aspidogaster conchicola. *Zool. Jahr. Anat.,* Bd. 9, 1896.
Tennent, D. H. A Study of the Life-history of Bucephalus, etc. *Quart. Jour. Micr. Sci.,* Vol. 49, p. 635, 1906.
Thomas, A. P. The Life History of the Liver-fluke. *Quart. Jour. Micr. Sci.,* Vol. 23, p. 90, 1883.
Young, R. T. The Histogenesis of Cyticercus pisiformis. *Zool. Jahrb. Anat.,* Bd. 26, p. 183, 1908.
Zeller, E. Untersuchungen über die Entwicklung und den Bau des Polystoma integerrimum. *Zeitschr. f. Wiss. Zool.,* Bd. 22, p. 1, 1872.
Zernecke, E. Untersuchungen über den feineren Bau der Cestoden. Jena, 1895.

THE AMERICAN TOAD (BUFO LENTIGINOSUS AMERICANUS, LeCONTE). II

A Study in Dynamic Biology

NEWTON MILLER

Clark University

Hibernation

Little is known about the toad during the winter. An anonymous article in *Cornhill* states that toads go down in the mud by ponds and become encysted in balls of clay. Allen is of the same opinion. More recently Gage says he thinks they go into the ground for hibernation and not under boards, stones, etc., as supposed. Toads were found under leaves in March, 1895, by Kirkland, who also states that they "do not hibernate singly, as a rule and it is not an uncommon thing to find in winter or spring a dozen or more closely packed together under a rock, board or in some other sheltered spot." Various individuals tell me that they have ploughed up toads in the fields or dug them up in gardens or flower beds in the spring. There is little doubt that in this latitude they normally pass the winter in the ground.

Toads bury themselves for the winter or often for the day in loose earth. To do this they always go down backwards. With a forward lateral movement of the hind feet the earth is pushed out and to either side and the body forced into the hole by the front legs. The loose earth falls over the head as the toad descends, thereby filling the burrow. In this way little trace is left to tell of the whereabouts of the toad.

It is probable that those found under leaves, etc., in early spring had emerged from winter quarters during a warm spell and had taken temporary refuge in such places.

Experiment No. I.

An experiment on hibernation was begun October 8. Holes twenty-eight inches deep were dug in three different localities. Into each hole was placed the four sides of a 14 x 36 x 36 inch cage made of $\frac{1}{4}$-inch-mesh wire netting. Then the holes and cages were filled to the level of the ground. Twenty toads were placed in each cage and a wire covering sewed on, thus making an enclosure without bottom, filled with soft earth and with a free space of eight inches between the ground and the top.

Cage *A* was placed on an exposed north slope of a hill beneath two pines. The slope at this point was probably 20°, therefore no water stood in or about the cage. The ground here is at least two thirds sand and gravel. Little protection was furnished by the pines, since their lowest branches were twelve to fifteen feet above the ground.

Cage *B* was located in a dry, well-sheltered place under the drooping branches of some spruces on a hill-side facing the east. So well was it protected that the sun never reached it and very little rain or snow. The ground at this point is a sandy clay.

Cage *C* was sunk under a maple tree in a place not more than four feet above the water in a near-by pond. No protection was furnished by the maple. Ashes, sand and loam in about equal parts composed the soil at this place.

The toads for this experiment were collected from the fourth to eighth of October. Each was weighed and marked by cutting off a toe. Those in *A* were put out the eighth of October and those in *B* and *C* the following day. One to several toads were found out of the earth in one or all the cages until November 26 with the exception of the twenty-ninth of October. My notes show a very slight tendency for those in cage *A* to hibernate before those of *B* and *C*.

After the twenty-sixth of November nothing was seen

of the toads until the twenty-eighth of March, when *A* was dug up, and eleven days later cage *C*. Fourteen were found in *A*, of which only three were alive. The depths at which they were found varied from one to twenty-four and a half inches. All above sixteen inches (the depth to which the ground was frozen) were dead. In *C* thirteen were found, of which nine were alive. There had been a trench dug near one end of the cage in the fall and the earth in this end was frozen to a depth of twelve inches. Two toads near the surface and two in the frozen end, one at a depth of twelve inches, were dead. Those alive were down below the frost line, which in this place was between eight and nine inches.

The accompanying table shows the weight of each live toad at the time it was put out and when dug up, also the depth at which it was found.

CAGE C

No. of Each Toad.	Weight, October 9.	Weight, April 4.	Depth in Inches.
1	50.5	44.0	15
3	19.5	15.0	9½
4	24.0	18.8	12½
5	27.0	25.6	14½
7	32.5	26.6	20
8	27.0	23.9	10
10	24.5	21.2	16½
12	5.5	4.6	11
19	19.5	15.8	15

CAGE A

No. of Each Toad.	Weight, October 9.	Weight, March 29.	Depth in Inches.
10	16.5	12.9	17½
18	9.5	7.0	17½
19	20.5	15.0	24½

Average loss of weight 3.8 grams.
The total loss of weight was 15.3 per cent. of total weight.

B was not disturbed, and the first toad to appear was no. 1 on the thirtieth of April, and the second and last was no. 7 on the twenty-eighth of May.

Experiment II

Another experiment was made on two toads which were placed in a 7 x 7 x 7 inch wooden box that contained some four inches of rather dry clay. A stone was laid on top and the box sunk ten inches in the side of a bank composed of clay and gravel. On the first of March, when the box was dug up, the ground all about it was frozen so hard that it had to be dug out with a pick. The earth in the box had been moist enough to freeze into clods, which were easily broken with the fingers. Both toads were alive, but no. 2 died two days later without showing any other signs of life than the beating of its heart. No. 1 moved her legs feebly as soon as broken out of the clay, had her eyes open in less than five minutes and within ten minutes more she was crawling about on the snow. Only the tips of some of her toes seemed to be frozen, but these never became sore. No. 2, as far as I could detect, was not frozen more than no. 1. No. 1 began feeding on the second day and during the remainder of the winter showed no signs of hibernating.

Experiment No. III

For this experiment a 12 x 12 x 24 inch glass aquarium was used in which was placed about three inches of moist earth. Six toads properly labeled were put in the cage, which was kept within eight inches of my radiator. As I was in my room most of the day and slept there at night I could watch them closely. I had a supply of meal worms, and every time a toad appeared it was given all it would eat. They came up usually about 8:30 P.M. and buried themselves by 10:00 P.M. Frequently they shed their skins and went down at once. No. 4 had the habit of only half burying herself and, probably, one fourth of the time was spent thus, but during this time she was rarely found sleeping.

The weight and sex of each toad was as follows:

No. 1, ♀ ..... 8.8 grams.
No. 2, ♀ ..... 27.8 grams.
No. 3, ♂ ..... 22.2 grams.
No. 4, ♀ ..... 76.5 grams.
No. 5, ♀ ..... 6.5 grams.
No. 6,[1] ♂ ..... 39.0 grams.

These toads were under daily observation from October 23 to April 1, excepting five days from December 26 to 30. Fig. 7 is given as an average month's record

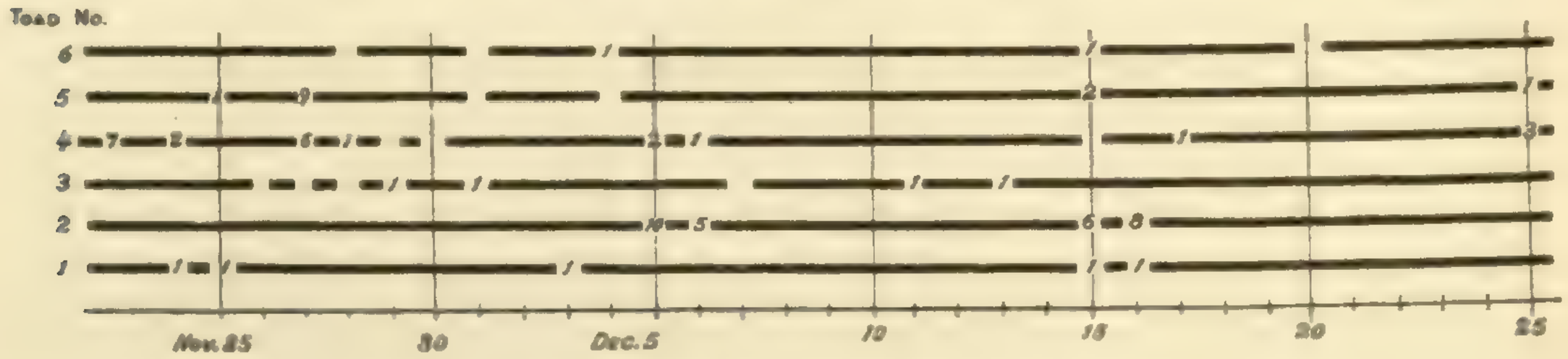


FIG. 7. Record of six toads for one month.

of this experiment. The continuous lines represent the time the toads spent under the earth; the breaks, the number of times the toads came up out of the earth; the figures in the breaks, the number of meal worms eaten at such times.

Experiment No. IV

This experiment was also carried on in my room, from the twenty-third of October until the eighth of April. During this time a female, weighing forty-eight grams, was kept in a small bell jar which contained, besides the toad, only a small thin piece of sponge. The sponge was kept moist and a piece of glass over the top of the jar prevented too rapid evaporation.

When the toad was placed in the jar she was cold, numb and to all appearances hibernating, but five hours after being brought into a warm room she was wide awake, and from then on to the end of the experiment was never seen with her eyes closed nor showing the least signs of hibernation. She fed throughout the winter, eating in all, the small number of 173 meal worms or their equiva-

[1] At the end of the experiment nos. 2, 5, 6 had increased their weight, respectively 7.4, 4 and 0.49 grams.

lent, but at no time did she go longer than nine days without feeding. Eight worms were the most she ever ate at one time, while one to three constituted her usual meal. She refused food during the day and fed only from 7 to 10 P.M.

Experiment No. V

This experiment is a duplicate of no. IV. with the exception that two small toads (about 8 grams) were used. The experiment began on the twenty-third of October and continued until the death of the toads, which, for the male, occurred December 15 and for the female, February 10. The female fed throughout this time with the exception of two periods, November 7–17 and December 18–February 10. During these two intervals she at times appeared to be hibernating or simply sleeping. It was almost a month before the male began feeding, but afterwards fed until he died. At no period did he show any tendency to hibernate. The male escaped from the cage and was found dried up. The female refused food from December 18 to February 10, became emaciated and died as though starved.

Conclusions

From experiment no. I, it is seen that toads go down into the ground to hibernate and that all of those not below the frost line in unsheltered places, perish.

Experiment no. II shows that toads in protected places can resist freezing temperature.

It is a question whether toads make any preparation at all for the winter more than simply burying deeper than they are accustomed to do in the summer. Experiment no. I shows that some had not hibernated as late as November 26. Toads are active until it becomes too cold for them to capture insects; as a cold wave comes, the toads for the first time begin to prepare for winter by digging a little deeper. As the ground gets colder,

they go further down, keeping a little below the frost line. I have found no evidence that toads select places in the fall and then proceed to bury themselves at once to a depth of eighteen to twenty-four inches.

Toads kept in a warm room do not have periods of torpidity. Boulenger says that batrachians never go into complete lethargy. The one in experiment no. IV was never asleep and those in experiment no. III were always wide awake and active when dug up. None of them became sluggish. The female of experiment V was, at times, during two periods seen with her eyes closed, but at these times she was easily awakened by a slight touch or a jar of the cage. At no time did she appear to be more than napping. All of the toads kept in my room fed throughout the winter, although eating only a small quantity. The period of least activity was from January 19 to February 19, when only one fed. Three of these toads fed eagerly during April, May and June.

There is no evidence that toads seal up their eyes, mouth and nostrils as a preparation for hibernation. Winter to the toad is only a long day, a suspension of work, a sleep. He is ready to begin his daily routine as soon as warmed up even in midwinter.

ENEMIES OF THE TOAD

When we consider the number of eggs laid and find that the number of toads does not increase, we are led to ask the question, What are the forces that keep the species in check? If we take the low figure of eight thousand eggs for an average spawn, then all of these—as well as all the eggs of the other spawns of a single female—or the toads that develop from them, except two, must meet a premature death in order that the species may just hold its own. This seems to be what is taking place with the toad.

What happens to this multiple of eight thousand eggs is partially known. There is no period from the laying

of the egg until death by old age that the egg, larva or toad is not subject to attack. I have found little evidence of the eggs being eaten in the ponds. Crayfish confined in the laboratory ate a few. Saprolegnnia destroy a small per cent. of the eggs, not by attacking the fertile ones directly, but by spreading from those that are decaying. The gelatinous sheath which envelops the delicate eggs is almost a perfect protection, but, as soon as the tadpoles wriggle out of it, they are preyed upon by fish, newts, crayfish, insects, and especially the predaceous aquatic larvæ of insects.

I give the results of my feeding tests to show how destructive some of the enemies of the tadpoles are.

Species.	No.	Time.	No. Killed.	Rate per Day.
1. Dragonfly nymph, Libellula sp.?	4	May 24–June 24.	500	4
2. Dragonfly nymph, sp.?	1	June 21–June 28.	37	4.5
3. Water beetle, Acilius sp.?	1	June 21–June 30.	40	4
4. Giant w. beetle, Dytiscus sp.?	4	May 9–June 23.	4,800	26.6
5. Water tiger, Dytiscus larva.	1	June 13–June 33.	425	42.5
6. Giant w. bug, *Belostome americanum.*	1	May 24–June 26.	360	11.2
7. Newts, *Diemictylus viridensens.*	4	May 8–June 19.	1,485	9
8. Crayfish, *Cambarus bartoni.*	1	June 1–June 24.	200	8.6
9. Leopard frog larva, *Rana pipiens.*	1	July 9–July 14.	66	8.8
10. Pickerel, Esox sp.? (four inches long).	1	June 22–June 24.	80	26.6

The above tests, with the exception of nos. 2 and 9, were made with tadpoles which were hatched from eggs laid about April 28. Since the transformation of the larvæ of this early laying began the twenty-second of June, it is seen that a portion of these tests were made with tadpoles almost ready to abandon the water. Those for no. 9 hatched on the twenty-fifth of June. No. 2 was fed for the first five days on tadpoles of the early spawn and the rest of the time on those hatched June 25. Only one tadpole a day was destroyed by this nymph during the first five days.

In treating the above data it must be taken into consideration that these tests were made in the laboratory and that tadpoles constituted the whole of the food of these animals during the tests. This is a very abnormal condition compared with that found in nature.

Two toads just metamorphosed were found in the stomach of a green frog about a week old. Mr. E. H. Eaton tells me of finding a toad an inch long in the stomach of a leopard frog. Adult toads could not be induced to eat the young. They would take them up, but immediately reject them.

The drying up of ponds during May and June kills great numbers of the tadpoles. More than 90 per cent. of the spawn is laid in the early spring when the ponds are full. The tadpoles migrate to the shallower water, where they find food and warmth. Here they crowd into small pockets, and as the water lowers are left in the isolated puddles to perish, unless timely rains refill the pond. The "drying-up process" is disastrous not only to the larvæ, but also to the toads. Great numbers just emerged are no doubt dried up before they find damp sheltered retreats. Adults also soon perish if deprived of moist places. I give the following to show the rapidity with which transpiration and absorption of water may take place in toads. A toad weighing 4.4 grams when placed in water, weighed 5.5 grams fifty-five minutes later. One hour later, after having been kept at a temperature of 85° F. in a box made of blotting paper, it weighed 4.8 grams. Another toad treated as above weighed 3.8, 4.5 and 3.8 grams, respectively. A third weighed 39.8 grams when placed in one fourth inch of water and 49.9 grams three hours later. This is a gain of 25 per cent of her first weight. This toad was capable of reducing her weight 8.7 grams by ejecting water. From these experiments it is seen how important moisture is to the toad and why toads seek damp places.

Birds play no small rôle in the destruction of the toad. Of the domestic varieties ducks, chickens and guinea fowls are always mentioned and to these Kirkland adds geese as feeding on toads, especially the young just as they are emerging.

"Crows, grackles and several species of ducks and herons," writes A. K. Fisher, of the Biological Survey, "are known to feed on small frogs and tadpoles, and undoubtedly do not discriminate in favor of toads." He presents further evidence to prove that the screech owl must be considered as a destroyer of toads. By stomach examinations of a number of crows, W. B. Burrows finds that the toad is a common article of food. Young partridges were tested on this point. They eagerly picked up the little toads, thereby killing them, but usually refused to eat them. Miss M. Morse reports the quail as feeding on young toads. As for predatory birds, the toad is an agreeable morsel of food. Mr. Fisher writes me that he has observed the broad-winged hawk feeding on toads while the latter were spawning. He also found "five stomachs of the red-tailed hawk, eight of the red-shouldered hawk, and five of the broad-winged hawk which contained the remains of toads." From the observations of Mr. F. H. Mosher, he states that "the marsh hawk is one of the worst enemies of the toad, destroying large numbers of them during the spawning season." He also states on the same authority that a toad was found in the nest of a Cooper's hawk.

Skunks and raccoons are the only mammals reported as feeding upon toads. Mr. E. H. Short writes that in his locality skunks destroy great numbers in the late fall, and that he found in October, 1904, the remains of seven toads which had been killed in one night (by a skunk?). His evidence on this point does not seem conclusive. Concerning raccoons, Dr. H. B. Davis occasionally feeds toads to those he has in confinement.

Professor Surface records twenty-seven species and varieties of serpents from Pennsylvania, of which ten feed on toads, and two others are suspected. The feeding habits of some of these have not yet been determined and it may be found that part of them use the toad as food. Toads constitute 41½, 20, 16 and 15 per cent. of the food, respectively, of the spreading adder

(*H. platirhinas*), the striped water snake (*R. leberis*), the common garter snake (*T. sirtalis*), and the spotted water snake (*N. sipedon*). The common garter snake and the spotted water snake are reported also as feeding on tadpoles.

Some of the game fish feed upon frogs and, presumably, they take toads also. Perhaps many toads are thus destroyed during the spawning season. We have reason to think that fishes feeding on insects and small fish devour tadpoles also. In pond no. 4 eggs were laid by the thousands and a large per cent. of them hatched, but not a single toad emerged. By the twenty-fourth of May not more than 200 tadpoles of the first laying remained and a few days later not one was to be found. There are fishes and crayfishes in this pond and the probabilities are that they destroyed the tadpoles.

Boys are very destructive to toads in the spawning season. This spring no less than one hundred and ten toads were killed about ponds nos. 1, 3 and 4. In 1897 Dr. Hodge records as one day's count two hundred dead about pond no. 4, and also that two boys had killed and carried away 300 from the same pond the day before.

Judging from my experiments, many toads die during the winter. As stated in the chapter on hibernation, sixty toads varying in size from 2 to 55 grams were put out in cages in the fall. Neglecting those under five grams (which I have reason to think escaped before cold weather) there were left fifty-one, of which only fourteen came out alive in the spring. This is a loss of 72.5 per cent., which surely must be above normal. However, further experiments and observations lead me to think that toads are killed if completely frozen. January 30, I permitted a toad 6.5 cm. long to bury itself in a cage containing a mixture of moist clay and loam. The cage was then subjected to a temperature of $-10°$ F. for twenty-four hours. At the end of this time the toad was frozen solid, and when thawed out showed no signs of life.

Another experiment, begun December 28, temperature 54° F., was made on five toads ranging between 3 and 7.5 cm. in length. These toads were put in a wire cage filled with leaves and then buried in leaves, which had drifted into an angle of a building. March 13, the cage was examined and all the toads found dead. These toads during this time had been subjected to several days of 0° F., weather.

On March 28 I examined a drift of leaves. Two dead toads were discovered half buried in the ground beneath leaves. There were about eight inches of leaves over them.

Contrary to these observations are those Kirkland, which might lead one to infer that toads can pass the winter successfully under leaves in this region. But as Mr. Kirkland's observations were made in March, and as toads in favorable springs emerge from their winter quarters in this month, we are inclined to believe that those he found under leaves had previously come out of hibernation and had taken temporary refuge where he found them.

The sewers of a town constitute a most destructive trap for toads. Sewer cleaners tell me that they take out "piles of toads" especially in the fall and spring. Examination of the "man holes" in May shows that there are on an average four toads in each one. At this rate, for Worcester alone, there are no less than 24,000 toads thus caught, which probably means their death also. It is making a low estimate to say that 50,000 toads perish annually in the sewers of Worcester. It is very probable that more adult toads in a city are killed by this means, alone, than by all others combined.

I give the following table as a rough estimate of the part that each known factor plays in holding the species in check.

Percentage of destruction until time of metamorphosis caused by:

Non-fertile eggs	15 per cent.
Drying up of ponds	25 per cent.
Insects, newts, fish, etc.	39 per cent.
Fungi	1 per cent.
Disease	5 per cent.
Total	85 per cent.

The remaining 15 per cent. may meet the following fate:

Drying up	20 per cent. = 3 per 100 eggs.
Domestic fowls and other birds	10 per cent. = 1.5 per 100 eggs.
Reptiles	6 per cent. = .9 per 100 eggs.
Boys	2 per cent. = .3 per 100 eggs.
Sewers, wells, etc.	15 per cent. = 2.25 per 100 eggs.
Mechanical means	10 per cent. = 1.5 per 100 eggs.
Winter	25 per cent. = 3.75 per 100 eggs.
Disease	3 per cent. = .45 per 100 eggs.
Miscellaneous (*including old age*)	9 per cent. = 1.25 per 100 eggs.
Total	100 per cent. = 15 per 100 eggs.

SUMMARY

B. l. americanus spawns from the latter part of April to the first of July.

This species lays in small ponds and only a portion of each is used as a spawning ground.

The males are the first to reach the water in the spring.

88.8 per cent. of all the toads in a pond at any given time are males. Males are in proportion to females as 80.7 : 100.

Trilling in the full vigorous voice is heard only during the mating season.

Females respond to the call of the males.

Males will not hold other males.

Spawn may be deposited at a depth of eighteen inches or more. This depth does not affect materially the hatching.

Fertilization takes place in an improvised basket formed by the hind feet of the male and the body and hind legs of the female.

85 per cent. of the eggs laid in natural ponds are fertile.

Oviposition requires six to eighteen hours.

The laying of two or four strands of eggs at a time can not be considered of specific importance.

Toads lay 3,900 to 15,800 eggs at one laying.

The eggs hatch in two to six days, depending upon the temperature.

Metamorphosis takes place in thirty-two to two hundred days.

On an average the tadpoles double their weight seven times in thirty-two days.

The tadpoles are omnivorous.

Toads feed entirely on animal matter. No food is taken unless it shows signs of life.

Toads refuse no insects, worms or slugs which they can swallow.

On an average toads feed only once in a day and a half.

The average amount eaten in a day by a toad is 1.12 grams.

About 80 per cent. of the toad's food consists of harmful insects.

Toads may be active from the latter part of March to the middle of November.

Toads are chiefly nocturnal.

Toads go into the ground to pass the winter.

The greater per cent. of those that do not get below the frost-line perish.

In the strictest sense of the term, toads do not hibernate if kept in a warm place.

Toads feed throughout the winter if kept warm, although eating comparatively little.

No preparation is made for the winter other than burying to a depth below the frost line.

Some toads do not hibernate until after the middle of November.

The eggs are seldom eaten by other animals.

Great numbers of tadpoles are destroyed by insects and insect larvæ.

Birds, fishes and reptiles feed upon tadpoles.

A large per cent. of the eggs and larvæ are killed by the lowering of the water.

Toads are destroyed, chiefly, by all classes of verte-

brates; by drouth and winter, and by the sewer systems of towns.

Literature

1876. American Encyclopedia, Vol. XV, pp. 777–9.

1899. Allen, G. M. Notes on the Reptiles and Batrachians of Intervale, New Hampshire. *Proc. Bost. Soc. Nat. Hist.*, Vol. XXIX, pp. 63–75.

1865. Allen, J. A. Catalogue of the Reptiles and Batrachians of Massachusetts. *Proc. Bost. Soc. Nat. Hist.*, Vol. XII.

1895. Assheton, R. Notes on the Ciliation of Ectoderm of Amphibian Embryo. Vol. XXXVIII, p. 465.

1892. Beddard, F. E. Animal Coloration. London, p. 159.

1894. Bos, J. R. Amphibia, Agriculture, Zoology, pp. 79–81.

1897. Boulenger, G. A. The Tailless Batrachians of Europe, Vol. I, pp. 23–67; Vol. II, pp. 221 ff.

1892. Boulenger, G. A. Poisonous Secretions of Batrachians. *Nat. Sci.*, Vol. I, pp. 185–190.

1896. Brimley, C. S. Batrachians found at Raleigh, North Carolina. Amer. Nat., Vol. XXX, p. 500.

1886. Brocchii, P. Crapud. Traité de Zoologie Agricole, pp. 240–242.

1833. Buckland, W. On the Vitality of Toads Enclosed in Stone and Wood. *Amer. Jour. Sci.*, Vol. XXIII, pp. 272–277.

1901. Conradi, A. F. Toads Killed by Squash Bugs. *Science*, Vol. XIV, p. 816.

1884. Cope, E. D. Batrachians of the Permian Period of North America. Amer. Nat., Vol. XVIII, pp. 26–29.

1896. Cope, E. D. The Geographical Distribution of Batrachians and Reptiles in North America. Amer. Nat., XXX, pp. 886–902 and 1003–1026.

1889. Cope, E. D. Batrachians of North America. Bull. U. S. Nat. Mus., No. XXXIV, pp. 277–281.

1907. Courtis, D. A. Response of Toads to Sound Stimuli. Amer. Nat., Vol. XLI, pp. 677–682.

1886. de Fischer, J. Rôle des Amphibians en Agriculture.

1906. Dickerson, M. C. Bufo lentiginosus americanus. The Frog Book, pp. 63–88.

1905. Ditmars, R. L. Batrachians of the Vicinity of New York City. *Amer. Mus. Jour.*, Vol. IV, pp. 186–190.

1898. Gage, S. H. The Life History of the Toad. College of Agriculture, Cornell University.

1898. Gage, S. H. Hibernation, Transformation and Growth of the Common Toad (*B. l. americanus*). *Proc. Amer. Ass. Adv. Sci.*, XLVII, pp. 374–375.

1901. Garman, H. The Food of the Toad. Ky. Agri. Exper. Station Bull., No. 91, pp. 62–68.

1902. Garman, H. Synopsis of the Reptiles and Amphibians of Illinois. Bull. Ill. State Lab. Nat. Hist., III, pp. 335–339.

1906. Hartman, F. A. Food Habits of Kansas Lizards and Batrachians. *Tr. Kansas Acad. Sci.*, XX, pt. 2.

1903. Hay, W. P. On Batrachians and Reptiles. *Forest and Stream*, LX, pp. 425–6.

1882. Hinckley, M. H. Mouth Structures of Tadpoles of Anurous Batrachian. *Proc. Bost. Soc. Nat. Hist.*, XXI, pp. 307–314.

1898. Hodge, C. F. The Common Toad. *Nature Study Leaflet*, Worcester, Mass.

1875. Huxley, T. H. Amphibia. Encyclopedia Britannica, 9th ed., I, pp. 750–771.

1907. Kellicott, W. E. Correlation and Variation in *B. l. americanus*. *Jour. Exper. Zool.*, IV, No. 4.

1901. King, H. D. The Maturation and Fertilization of the Egg of *B. lentiginosus*. *Jour. Morph.*, XVII, pp. 293–330.

1907. King, H. D. Food as a Factor in the Determination of Sex in Amphibians. *Bio. Bull. of Marine Bio. Lab.*, XIII, No. 1, pp. 40–56.

1904. Kirkland, A. H. The Habits, Food and Economic Value of the American Toad. Mass. Agri. College Bull., No. 40.

1882. Legrips, M. V. Vitality of Toads. *Knowledge*, I, p. 202. (This is probably Buckland's experiment and misquoted, as the same experiments are given with the same result. See "Cosmos.")

1904. Morse, M. Batrachians and Reptiles of Ohio. Bull. Ohio State Univ., Series 8, No. 18, pp. 96–123.

1871. Putnam, F. W. Some Statements concerning the Frogs and Toads found at Cambridge, Mass. *Proc. Bost. Soc. Nat. Hist.*, IX, pp. 229–230.

1888. Ryder, J. A.. "Ventral Suckers" or Sucking "Disks" of Tadpoles of different Genera of Frogs and Toads. AMER. NAT., XXII, p. 263.

1901. Sharp, D. L. Wild Life near Home, p. 313.

1905. Short, E. H. Editorials (on Skunks). *Oologist*, XXII, pp. 132–135. and 188–190.

1900. Slonaker, J. R. Some Observations on the Daily Habits of the Toad (*B. lentiginosus*). *Ind. Acad. Sci.*, pp. 167–170.

1906. Stone, W. Amphibians and Reptiles of New Jersey, Pennsylvania and Delaware. AMER. NAT., XL, pp. 159-170.

1863. Verrill, A. E. Catalogue of Reptiles and Batrachians found in the Vicinity of Norway, Maine. *Proc. Bost. Soc. Nat. Hist.*, IX, pp. 195–199.

1882. Yarrow, H. C. North American Reptiles and Batrachians. Bull. 24, U. S. Nat. Mus., pp. 166–167.

OBSERVATIONS ON COPULATION AMONG CRAWFISHES WITH SPECIAL REFERENCE TO SEX RECOGNITION

DR. A. S. PEARSE

UNIVERSITY OF MICHIGAN*

DURING the past winter the writer kept about three hundred crawfishes in aquaria for a couple of months and had opportunity to observe their copulating reactions from time to time. As the published statements in regard to sex recognition in the genus Cambarus are somewhat meager, the results of some of these observations may be of interest. The species represented in the aquaria were, *Cambarus blandingi acutus* Girard, *C. diogenes* Girard and *C. virilis* Hagen. Most of the observations here recorded were made upon the last-named species, but nothing was observed in the behavior of the others to make it appear that there was any essential difference in the mating reactions of these forms.

Andrews[1] was the first to give a careful account of copulation in the genus Cambarus. He discovered that while the male holds the female on her back beneath him a spermatophore is transferred from his abdominal appendages to the cavity within the annulus ventralis of the female, where it remains sealed up until the eggs are laid. Andrews gives an excellent account of the details of the process but refers only indirectly to sex recognition. He remarks (p. 868):

When a male is put into a vessel with a female he seems ere long to become aware of the presence of the female and does not act as he does when only males are present. The female generally retreats and may

* Contributions from the Zoological Laboratory of the University of Michigan.

[1] Andrews, E. A., "Conjugation in an American Crayfish," AMER. NAT., Vol. 29, 1895, No. 345, pp. 867–873.

even resist the attacks of the male, but generally this is not done with much vigor, and very soon after being seized by the male the female passes into a state of passivity, resembling death.

Hay[2] in a recent paper makes statements which give a somewhat different aspect to the matter. In speaking of an hermaphrodite crawfish he says (p. 228):

> It might be added that during the time the specimen was kept alive it was seen in conjugation with a female of the same species and a little later was itself seized and held for a short time in the usual manner by a male. The latter, however, is a matter of little importance, as I have several times observed the same thing in the case of two males neither of which was hermaphrodite.

An adult male of the genus Cambarus is easily distinguished from a female of the same species by his larger chelæ and narrower abdomen, and the sex of any individual can of course be accurately determined by examining the first two pairs of abdominal appendages. Whether such differences are as readily discriminated by the sensory receptors of a crawfish as they are by the human eye is perhaps open to question. According to the quotation from Andrews it would appear that a male is able to recognize a female as such, but the statements of Hay might be interpreted in such a way as to lead to the opposite conclusion.

A series of five experiments was carried out to test the ability of male crawfish to discriminate members of the opposite sex. In the different experiments from two to seven males were separated from females which they had been holding and put together in a flat circular dish (which measured thirty centimeters in diameter and contained clean water to a depth of about five centimeters). After such treatment the crawfishes were active for a time and moved restlessly about the dish. During this period of activity one male often tried persistently to copulate with another male, but such attempts were always resisted, and, although individuals were turned

[2] Hay, W. P., "Instances of Hermaphroditism in Crayfishes," Smithonian Misc. Coll., Vol. 48, 1905, Pt. 2, No. 1593, pp. 222–228.

over in some cases, they always eventually succeeded in freeing themselves. After these males had been allowed to "fight" thus among themselves for from half an hour to two hours (the time varied in different experiments) they became comparatively quiet and finally came to rest in a group at one side of the dish in such a way that their bodies were in contact with each other. After they had remained in this condition of rest for at least half an hour a female which had just been released from copulation with a different male was gently introduced into the dish with them.

In all five of the experiments the female moved about the dish and came in contact with one or more of the males, and sometimes she even walked over them, but nevertheless there were only two attempts at copulation within half an hour after a female had been placed in the dish. In one of these cases a male attempted to grasp another male after the female had been introduced, but he soon desisted from the attempt and all the individuals in the dish then became quiet again. In the other instance one of the (two) males attempted to turn over the female as soon as she came in contact with him (not as soon as she was introduced into the dish). These experiments showed that males which had recently been in active copulation were not necessarily induced to copulate again by the immediate presence of an active female.

Five other experiments were performed which were similar to those just described except for the fact that the female was introduced into the dish with the males before they had come to rest. In this second series copulation took place within half an hour in every case. The results make it appear that the readiness with which copulation is undertaken by a pair of crawfishes depends upon the physiological state of the male, for, as Andrews has stated, the male usually takes the active part in the mating reactions, while the female remains passive.

Another series of observations showed that the readiness with which copulation takes place depends largely

upon the "chance" coming in contact of two individuals which are in proper physiological state. On five different occasions when the aquarium, which contained two hundred crawfishes, was visited and no pairs were found to be copulating or attempting to do so, all the individuals were dragged into the center of the aquarium and heaped together in a pile. They were then allowed to remain undisturbed for half an hour. During this time there was an active scramble and many individuals necessarily came in contact with each other. In all the experiments from three to five pairs were found to be in copulation at the end of the half hour. These observations showed that individuals had been present in the aquarium which were in the proper physiological state for copulation, for as soon as they came in contact with each other the usual mating reaction took place.

There are many factors which might possibly exert an influence on the copulatory reflexes of a crawfish and it is easily conceivable that such stimuli as temperature, light and chemical substances might be of importance in this connection. In regard to temperature Bell[3] has observed (p. 625) that, after a number of individuals had been warmed,

> The males showed marked sexual activity, rushing up to the females, pushing them about, seizing them and trying to turn them over in spite of their vigorous resistance. One of the males did succeed in turning a female on her back twice, although she struggled violently to escape—a thing which a female never does in the ordinary sexual act.

He concluded that, "the rise of temperature seemed to stimulate the males to sexual activity but not the females." During the present experiments it was observed that there were fewer cases of copulation when the temperature of the water in the general aquarium was below 11° C. than when the temperature was above that point. Apparently temperature is of some importance as exerting an inhibitory or excitatory action on the copulatory impulse.

[3] Bell, J. C., "Reactions of the Crayfish," Harvard Psychol. Ser., Vol. 2, 1906, pp. 615–644.

Chidester[4] has recently shown that the general activity of crawfishes is greater at night and it would therefore seem probable that copulation would be more likely to take place in the dark than in the light. In order to ascertain if this supposition was correct, two oblong dishes were placed side by side in front of a window and were filled to a depth of five centimeters with water which was of the same temperature in the two dishes (11° to 14° C. in different experiments). One of the dishes was allowed to remain exposed to strong light, but not to the direct rays of the sun, and the other was completely enclosed in a tight wooden box which was painted black on the inside and covered by a movable lid. In each experiment two pairs of crawfishes which had been copulating or attempting to do so were isolated and a separate male and female placed together in each dish, after which their behavior was noted at short intervals of time. In order to eliminate the effects due to the individuality of any particular crawfish, the individuals of each quartette were changed about as much as possible in successive trials. After the first copulation, the male was changed from the dark dish to the one in the light, and the male which had been in the light took his place; after the next trial the pairs were interchanged, and finally the two females were changed about. By this method of procedure there was an opportunity to compare the rapidity of copulation in the light and in the dark. The results of the experiments are given in Table I.

TABLE I.

Showing the results of seven experiments to ascertain whether certain crawfishes would copulate more quickly in dark or in light. (L indicates that the pair in the light copulated first; D, the pair in dark copulated first; E, both pairs copulated at the same time.)

Experiment.		1	2	3	4	5	6	7
Trial 1		L	D	L	L	L	D	D
Trial 2	♂ ♂ interchanged	D	E	D	L	L	L	D
Trial 3	Pairs interchanged	L	L	D	D	D	D	D
Trial 4	♀ ♀ interchanged	L	E	L	D	L	D	D

[4] Chidester, F. E., "Notes on the Daily Life and Food of Cambarus bartonius bartoni," AMER. NAT., Vol. 42, 1908, No. 503, pp. 710–716.

In twelve of the trials copulation took place first in the light; in fourteen cases the pair in the dark copulated first, and in the other two instances the two pairs occupied the same period of time in becoming united. Twenty-eight different individuals were given twenty-eight opportunities to copulate and approximately an equal number of "first" copulations took place in the light and the dark. From these experiments it appears that conditions of light stimulation are apparently of little consequence, at least where individuals which are in a state of excitement are concerned.

Attempts were made to arouse males to a state of activity by adding extracts to the surrounding medium. The males were separated from their mates and allowed to become quiet in a dish of clean water. Various portions of females which had been recently copulating were then added, and although pieces of ovary, pieces of abdomen and extracts from these organs and from the whole body were used in this way, nothing but negative results were obtained. The males remained quiet and exhibited no signs of excitement within half an hour after the portions of the female's body had been added. From these results it does not seem probable that copulation is brought about by the action of any secretion given off by the female which might serve to excite the male.

The results of all the experiments described indicate that sexual union is more or less a matter of chance. If a male and a female which are in the proper physiological condition come together they will copulate with equal readiness in the light or dark. Neither sex can be said to be wholly responsible for the act of sexual union and although the male usually assumes the active part, it is not an invariable rule. An instance was observed in which one female fought almost continuously with another for over two hours. When this pugnacious individual was placed in a dish with several males she walked about actively and grasped them with her chelæ, but as soon as one of them grasped her and attempted to turn her over,

she became quiet and was soon in copulation. If we examine Table I it will be seen that in experiments 1 and 6 the same male copulated first in four of the trials, but in experiments 2, 4 and 5 the male which copulated first in trial 1 was equalled or excelled by the rival male in the three succeeding tests. No female copulated first in all four trials.

In all the observations cited no evidence was seen which would go to show any power of sex descrimination in the crawfish. During the mating season the instinct of the male is to grasp and turn over every crawfish which comes in his way. The method is one of trial and the result of such random movements depends largely upon the reactions of the individual with which copulation is attempted. If this individual is a female of the same species the attempt may meet with success but if it is a male or a female of another species the effort at sexual union is usually of short duration. The lack of discriminative ability on the part of the males is shown by the fact that they often attempt to copulate with individuals of their own sex. This fact in itself is not of course very conclusive as similar behavior is often observed in many higher animals, such as dogs and cattle, in which the males are doubtless able to recognize the females as such. Furthermore, on two occasions males were observed to be in copulation with females which had been dead for twelve hours and in another instance a male of one species (*Cambarus virilis*) was found in copulation with a dead female of another species (*C. blandingi acutus*). This last observation is of especial interest for, as Andrews[5] says (p. 474) it is not known "whether the male stylets and the female annulus are closely adjusted to each other in each species or not. Experiments should at least decide whether the males of one species can fill the annuli of other species or not." The observation just cited shows that two different species can at least

[5] Andrews, E. A., "The Annulus Ventralis," Proc. Boston Soc. Natur. Hist., Vol. 32, 1906, No. 12, pp. 427–479, pl. 43–48.

unite sexually as I was careful to observe that the stylets of the male were actually inserted into the annulus of the female. Whether a spermatophore can be transferred under such circumstances is of course still a question.

The observations described in this paper would lead to the conclusion that the crawfishes have little or no power of sex discrimination. The male "tries" every crawfish which he meets and the instinct of the female is to remain passive under such treatment while another male will attempt to escape. The sexes come together as the result of random movements or in the course of the daily travelling about in search of food. Holmes[6] reached similar conclusions as a result of his observations on amphipods. Male amphipods, however, would not attempt to copulate with a dead female and in this respect their powers of discrimination apparently excel those of the crawfish.

[6] Holmes, S. J., "Sex Recognition among Amphipods," *Biol. Bull.*, Vol. 5, 1903, No. 5, pp. 288–292.

SHORTER ARTICLES AND CORRESPONDENCE

DEGENERATION ACCOMPANYING INBREEDING

It seems now generally conceded that inbreeding per se is not injurious but that when a similar defect in the germ plasm comes from both sides of the family the children do not rise in respect to this character above the parental level. The effect of close inbreeding in small isolated communities is, at any rate, always interesting, and affords an excuse for the following note, based on facts gleaned from a letter sent me by Rev. H. East, a missionary whose headquarters are at Haka, Chin Hills, Burmah.

Rau Vau village has been isolated for about seven generations. It contains about sixty houses and possibly two hundred inhabitants. Of these ten are idiots, many are dwarfs and some hydrocephalic. A number of cases of syndactylism and brachydactyly occur. Mr. East was not able, offhand, to state how these peculiarities are inherited, but it is to be hoped that he will be able to report on this subject later. Certainly, heredity in such a community deserves careful attention.

C. B. Davenport.

A NOTE OF THE PRAIRIE-DOG OWL WHICH RESEMBLES THE RATTLESNAKE'S RATTLE

In looking over an earlier number of the American Naturalist[1] I find a note under this head by F. B. Loomis in which he describes a note of the adult burrowing owl which so closely resembled the rattle of a rattlesnake that not only the members of his party, but their horses as well, were deceived.

> . . . it alighted and began a third rattle; and this time all saw its stretched neck, bulging eyes, open beak and vibrating tongue. The whole appearance of the bird indicated assurance that it would thus frighten off any enemy; and it certainly deceived the four plain-bred horses, as well as the men, all of whom had for weeks been familiar with rattlesnakes, and two of them for years.

This reminds me that about sixteen years ago I made some observations on the same subject. It is particularly interesting

[1] Am. Nat., Vol. XLI, pp. 725–726, 1907.

to me to note that the horses were invariably frightened by the "rattle," for in thinking of my own experience I have often considered that perhaps my observations were somewhat prejudiced that rattlesnakes are so popularly supposed to occupy the holes with the owls. The observations which Loomis records here were for an adult bird, while mine were upon the young.

A burrow was dug out and a nest of eight young secured. When taken from the burrow, and with great frequency, these young birds—still in the downy condition—made this sound. As I remember it, this occurred every time they were disturbed. These birds were taken in Cheyenne or Rawlins County, Kansas, while Loomis's observations were made in Wyoming. Loomis seems to regard the note as peculiar to the one individual he observed, for he writes:

> If it succeeds in teaching this trick to its young, a protective habit of great value will be formed.

Whether the prairie-dog owl generally has this note I am quite unprepared to say, but my observations in northwestern Kansas indicate that it is not an individual peculiarity. It is so easy to attribute adaptive significance to characters that our attitude toward such suggestions should always be very critical; whether the note described is ever of any service to the bird would be a difficult problem for a field ornithologist. It would be interesting to know whether notes of this kind are peculiar to the prairie-dog owl, or whether they are also heard in species which have no possible association with the rattlesnake. Some one familiar with birds in the field could probably answer this question.

J. Arthur Harris.

NOTES AND LITERATURE

THE CAUSATION OF SEX[1]

This book is the work of a general practitioner of medicine. For twenty years he has collected clinical facts and materials upon which he now claims to have built up a new theory of sex. The theory has been put to the test in forecasting the sex of the unborn child and proved adequate in 97 per cent. of cases. The cause of sex being known in man, the determination of sex is readily accomplished. A summary disposition of Schenk's once-famous superior-vigor-theory is made by simply citing the clinical fact of the occasional simultaneous birth of both a boy and a girl.

The theory dissociates absolutely the male parent from any influence in sex causation—thus differing from several otherwise closely similar hypotheses. It is simply that "sex depends upon which ovary supplies the ovum fertilized." The clinical materials employed in proof are: (1) Sexually differing families; (2) extra-uterine pregnancy; (3) pregnancy in double uteri; (4) multiple pregnancy; (5) migration of ovum (internal and external; (6) preponderance of male over female births. Furthermore, the author denies validity to all arguments, respecting sex in man, from analogy with invertebrates or even lower vertebrates, believing "women not analogous to any living thing."

Respecting the anatomy and physiology of the female generative organs the following facts are noted and employed in the construction of the theory: (1) Lower position in pelvis of right ovary and internal opening of right oviduct; (2) larger caliber of right oviduct; (3) larger size of right ovary; (4) occasional presence of two ova in a Graafian follicle; (5) recorded cases of double nuclei in the mammalian egg; (6) corpus luteum as indicator of ovary from which the impregnated ovum came; (7) dependence on common cause, consequently close coincidence, of ovulation and menstruation (proof: scars of corpora lutea correspond to the number of menstrual periods experienced). The

[1] "The Causation of Sex," by E. Rumley Dawson, London, H. K. Lewis, 1909, pp. 190, 21 illustrations.

foregoing statements are supported mainly by quotations from various recognized authorities.

Chapters 3 and 5, dealing with the Formation of the Ova and Fertilization respectively, are vulnerable at various points to the criticisms of gratuitous assumption, specious reasoning and flagrant disregard of recent biological advance, more particularly respecting the questions of heredity and sex. Absolutely no notice is taken of the work of Bateson, Davenport and Castle on Mendelian inheritance, nor of the cytological and experimental results concerning the determination of sex respectively of Wilson and Correns. But however scant the appreciation of the bearing of results from non-human materials on the general problem, and however radical the ideas here expressed, the theory as such remains essentially unaffected.

In chapter 3 it is urged that "Each ovum has its own definite and unalterable sex, being either male or female according to the ovary from which it is derived." Though microscopic evidence of such difference is not yet forthcoming it is asserted to obtain "just as between the eggs of two different women." "Similarly the ovum of a negress is indistinguishable by our present appliances from the ovum of a blonde, yet we know full well that if fertilized one produces a black child while the other gives rise to a white one" (p. 29). Assuming, as this line of reasoning does, that there is identity (or at least close similarity) between the process of sex-inheritance and color-inheritance, both would seem to be due, in a large measure, to the influence of the male. For the ovum of a negress fertilized by the spermatozoon of a blonde male might give rise to a black child, but it would more likely be a mulatto, perhaps almost indistinguishable from a blonde—similarly sex may be influenced or determined by the spermatozoon.

Identity in the mechanism of heredity, whether it concern sex, color or other unit characters, is widely accepted; but Dr. Dawson seems to posit such identity or the absence of it depending upon the conclusion he desires to reach. Above he posits identity: but he reasons incorrectly in an attempt to reach a desired conclusion.

In a later chapter (chapter 5), starting with the assumption that the "provision in the human ovum of multiple avenues of entrance (the radiating pores of the zona pellucida) looks as though multiple spermatozoa are required to enter thereby in order to fertilize the human ovum," he argues that the "differ-

ent number of paternal and maternal features and characteristics inherited by the respective children must be due to a varying quantity of the paternal body or germ-plasm carried to each ovum fertilized by the varying number of spermatozoa'' (100 or more). He argues for the necessity in human fertilization of multiple spermatozoa on the basis of (1) prolific supply at each ejaculation (200,000,000—Lode); (2) very frequent renewal; (3) long life in oviduct. According to this argument the color of the child resulting from the development of the egg of a blonde fertilized by the spermatozoon of a negro would be blonde if only one sperm entered, black if many entered—the direct contrary of his former position.

Again, the author holds that there is no question of heredity or ''the exhibiting of ancestral tendencies or peculiarities in a varying degree'' among the invertebrates! All that is necessary here at fertilization is to provide stimulus to development; consequently one spermatozoon will do. Even among cod or herring one sperm is held to be sufficient for the same reason. The number of spermatozoa demanded for the expression of any particular degree of inheritance is believed to be indicated by the number of micropyles in the egg. If always only one, or the same number of spermatozoa, entered the human ovum there could be no such thing as somatic variation. Evidently our author knows little of the later studies on the nature of fertilization and the function of the chromosomes in relation to sex and general inheritance. It is stated that ''many spermatozoa entering the ovum lead to a father-like child whether boy or girl; a few only entering leave the yolk still maternally superior or prepotent so that the child whether boy or girl takes after the mother'' because it is too much to ask of a single chance spermatozoon ''besides fertilizing the ovum nucleus, also . . . to settle the sex of the coming child and likewise impart to the oosperm the form and face, talents and tendencies, coloration of hair, skin and eyes, movements and mannerisms, and even diseases of the father'' (p. 42). And yet by the hypothesis that in the chromosomes of a single spermatozoon reside such potency can be explained the various phenomena of Mendelian inheritance —moreover, characters can be added and subtracted in accord with this theory. How could the phenomenon of color dominance in mice and guinea-pigs be explained on Dawson's assumption? Of course he will always reply that there is no

analogy between heredity in guinea-pigs and the human female. Evidently he has not yet accepted even the fact of evolution.

Absolute identity of the process of fertilization is asserted to be disproved by the results of merogony. The connection is obscure, but if the findings of Boveri and Delage in echinoderms have any bearing on the matter it would be to show that a single spermatozoon is prepotent over the greater extranuclear mass of the ovum and determines an organism with male characteristics.

Similar examples of loose reasoning and unwarranted statement appear in chapter 6. Here it is said that it is "reasonable to suppose that the association of the left ovary with the production of the female sex is due to the fact that the weaker sex should result from the weaker side of the body." How will Dr. Dawson prove that the female is the weaker sex, or that the left side of the brain is the weaker, or that left-handed persons are weaker on that side? "To inquire why the ovary of the right side should have been chosen for the production of boys rather than the other side seems as fruitless and as useless as to inquire why the liver should have been placed to the right and the spleen to the left of the body." Surely this is giving a curious turn to the method of reasoning by analogy. The position of the liver and spleen, as also of the stomach and other viscera, is determined largely by the mechanical factor of pressure under which they mutually adapt themselves to their narrow confines. Originally they also were symmetrically placed with respect to the body axis as are the gonads and kidneys which remain so definitively. With as much reason might one argue that the right eye sees only the upper colors of the spectrum and the left the lower, or that one kidney secretes the mineral and the other the organic matter of the urine or that the right testicle gives rise to blondes and the left to brunettes.

All this, however, has little bearing on the essential point of the theory, which is based upon the following facts and cases: (1) Woman has one-sexed children only by different men; (2) father produces both-sexed children with different wives but only one sex with each wife (in both of these instances the woman is supposed to be unilaterally sterile); (3) man gets both-sexed children with one of his wives but only one sex with the other "because she is unilaterally sterile." If it depended on the male, it is argued, he should get both-sexed children with both wives. The theory is further supported by animals also: (1) cow covered by fifteen bulls has seventeen calves, all female;

(2) mare covered by more than six different stallions had ten foals, all male; (3) bitch covered by two different stud dogs gave birth in two litters to six male dogs; (4) sow gave birth to a litter of ten boar pigs. In all these cases the female is supposed to have been unilaterally sterile. One might urge against the cogency of these facts as supporting the theory that the law of probability and the hypothesis of Mendelian dominance could explain them as well as the supposition of unilateral sterility.

In chapter 8 cases of pregnancy are reported to prove the theory. The proof here consists in showing cases of male and female pregnancy with the corpus luteum in the right and left ovum respectively; six cases of the former are given, and three of the latter (one doubtful). Among the vast number of possible cases, these eight might very well be mere coincidences—for when exceptions occur he invokes the aid of a migration of the ovum.

Chapter 9 considers cases of extra-uterine pregnancy to prove the theory. Twelve cases are reported of tubal pregnancy and a corpus-luteum-bearing ovary on the same side. Accordingly, if pregnancy be in the right oviduct and the fœtus a male, one is justified in declaring the ovum came from the right ovary. Nine such cases are described; and five in which a female fœtus was found in the left oviduct. Furthermore, two cases of twin-pregnancy, one extra-uterine and the other intra-uterine are shown to conform to the rule. Dr. Seligson of Moscow, is said to have collected fourteen cases of males developing in the right tube and females in the left. Two cases of right ovarian pregnancy of male sex are given, and one reverse case.

Chapter 10 takes up cases of pregnancy after unilateral ovariotomy Five examples of male births after removal of the left ovary are submitted, and four where females were born after the right ovary was removed. A case is reported of right ovariotomy combined with resection of the left ovary, followed by the birth of a girl. Many exceptions are admitted, but they are ascribed to incomplete removal of the ovary in question, or the regeneration of ovarian tissue from the pedicle, or to the presence of an accessory ovary. Thus these examples lose much of their force.

Cases of pregnancy in abnormal uteri are discussed in chapter 11. Seven cases are recorded, four in which the right halves of double uteri were pregnant with males, and three where the left halves contained females. Exceptions, which are frequent, are

charged to a migration of the ovum from one side to the horn of the opposite side. And "in those animals such as pigs, cats, rabbits and mice—whose offspring are truly multiple—the fœtuses are mixed up in the two cornua; but . . . . . the ovaries contain between them a corresponding number of corpora lutea, both individually as regards sex and collectively as regards number" (p. 98).

An interesting presentation is given in chapter 15 of supposed reasons why more boys are born than girls. Statistics recorded for over 200 years show this to be a fact, the proportion being 106 males to 100 females. More boys are said to be born by reason of the greater number of male eggs liberated, and by reason of easier access of spermatozoa to male ova, both due to the anatomical facts above enumerated. Nature thus attempts to compensate for the greater male mortality at birth and during the first five years.

Multiple conceptions are brought under the hypothesis. The woman is held responsible for plural pregnancies; nevertheless the author is forced to admit exceptional cases (p. 144).

In chapter 22 Dr. Dawson attempts to analyze the more obvious objections to his theory. To the criticism that it is too mechanical he answers that all life is essentially mechanical, *e. g.*, respiration, circulation, menstruation. With the fact that the majority of birds have only one ovary, yet the hen lays eggs of both sexes, he has considerable trouble. But he makes argument impossible by simply stating that woman is not analogous to the hen. He seeks support for this contention by citing the fact that birds are asymmetrical in other respects, *i. e.*, absence of right carotid artery and right jugular vein, adding that it is "no more necessary to assume identity between birds and women in the matter of the causation of sex, than in the matter of circulation." It must be pointed out that originally (before hatching) both the circulatory and reproductive systems of birds are identical, at least as concerns bilateral arrangement, with those of the human embryo. It seems more reasonable, on the basis of comparative embryology and physiology, that the human ovaries have an identical, interchangeable and compensatory function just as the kidneys, the testes, the eyes and the ovaries, as respects menstruation, are known to have.

The two concluding chapters deal with the problem of forecasting sex and the production of sex at will. Knowing that the gestation period is 40 weeks and that 13 ovulations normally

occur per annum and that the ovaries normally function alternately, one need know further merely the date of birth and sex of the previous child to compute the sex of the coming child. It is evident that the ovulation in the same months varies in successive years (due to the fact that there are 13 ovulations). From this point then we can work to the tenth month previous to the expected birth. Hence "if children are born in the same month an odd number of years apart they are of opposite sex; if an even number of years intervenes they are of the same sex" (p. 183). Accordingly then the "production of sex at will must consist in avoiding any attempt at fertilization in the months during which an ovum is produced of the sex not desired. Dr. Dawson believes it possible that some day by means of some modification of the Röntgen or other rays, we may actually see an ovary ovulate. At present there appears no way of determining the sex of the first-born.

The book as a whole furnishes entertaining and suggestive reading. One leaves it unconvinced, but stimulated perhaps to test the theory by careful observations of his own clinical materials. One feels, however, that the author is not justified in his extreme position that even higher vertebrates can teach us nothing with respect to the cause of sex and heredity in man. Surely one trained in general biology, especially cytology and comparative embryology can not accept the "theory" as anything more than an unverified hypothesis. Of course the array of clinical facts at first seems to give the theory a semblance of solidity; but this is rapidly dispelled by the arbitrary disposition made of numerous exceptions. By the same methods it would probably be as easy to prove the reverse position, *i. e.*, that females come from the right ovary and males from the left. The problem of sex can never be solved by the method of collecting clinical materials alone—and Dr. Dawson's book represents perhaps the last effort at such a solution. Clinical materials will always be valuable adjunets, but the essence of sex resides probably as much in the male gametes as in the female, and its final elucidation seems indicated along the lines of a cytological (chromosomal!) interpretation of Mendelian phenomena.

H. E. JORDAN.

INDEX

NAMES OF CONTRIBUTORS ARE PRINTED IN SMALL CAPITALS

ALLEN, ARTHUR, and ALBERT H. WRIGHT, Early Breeding Habits of Amblystoma punctatum, 687
ALLEN, J. A., Osgood's Revision of the Genus Peromyscus, 633
Amblystoma punctatum, ALBERT H. WRIGHT and ARTHUR ALLEN, 687
American Toad, NEWTON MILLER, 641, 731
Anatomy, Plant, Progress during the Last Decade, EDWARD C. JEFFREY, 230
ANDREWS, E. A., A Male Crayfish with some Female Organs, 461
Ants, Outfit for the Study of, EDITH N. BUCKINGHAM, 611
Apodous Holothurians, H. L. Clark on, W. K. FISHER, 111
Archegoniates, Schenck on the Origin of the, BRADLEY M. DAVIS, 107
Arid Regions, Local Distribution on, VOLNEY M. SPALDING, 472
Armor Plates, Dinicnthyd, BURNETT SMITH, 588
Armsby, H. P., Feeding for Meat Production, RAYMOND PEARL, 309
Artifacts of Breeding, Pure Strains as, O. F. COOK, 241

Bactmetjew's Experimentelle Entomologische Studien, FRANK E. LUTZ, 55
Batrachoceps attenuatus and Autodax lugubris in Southern California, WILLIAM A. HILTON, 53
Bauer, E., on Unit Characters, W. J. SPILLMAN, 243; A Case of Non-Mendelian Heredity, W. J. SPILLMAN, 437
Bee, Honey, Color Sense in the, JOHN H. LOVELL, 338
Behavior of the Domestic Fowl, PHILIP B. HADLEY, 669
BERRY, EDWARD W., Pleistocene Swamp Deposits in Virginia, 432
BESSEY, CHARLES E., In Memoriam Leo Errera, 640
Biometric Constants, Accuracy of the, RAYMOND PEARL, 238
Biometrics, 238, 302
Bohn's The Birth of Intelligence, H. S. JENNINGS, 619
Breeding, Experiments with Rats, T. H. MORGAN, 182; Pure Strains as Artifacts of, O. F. COOK, 241; Selection Index Numbers and their Use in, RAYMOND PEARL and FRANK SURFACE, 385
Broili on the Age of the Gaskohle, ROY L. MOODIE, 122
Brooks, W. K., and B. McGlone, Lung of Ampullaria, WILLIAM E. RITTER, 695
BUCKINGHAM, EDITH N., Outfit for the Study of Ants, 611
Bufo lentiginosus americanus, LeConte, NEWTON MILLER, 641, 730
Burnett, E. A., The Breaking Strength of Bones, RAYMOND PEARL, 309
Butterflies, Blue, of the Genus Celastrina, T. D. A. COCKERELL, 114

Cænolestes, Polyprodonta and Piprodonta, PAULINE H. DEDERER, 614
Camel from the Lower Miocene of Nebraska, HAROLD JAMES COOK, 188
CAMPBELL, DOUGLAS HOUGHTON, The New Flora of Krakatau, 449
Canadian Oyster, Larva and Spat of, J. SAFFORD, 31
CASTLE, W. E., Coat Colors in Rabbits, T. H. Morgan, 504
Categories of Variation, S. J. HOLMES, 257
Cestodes, of Birds, HENRY B. WARD, 62; and Trematodes, The Cuticula and Sub-Cuticula of, HENRY S. PRATT, 705
Chadwick, H. C., Red Sea Crinoids, AUSTIN HOBART CLARK, 253
Chambers, Robert, Size of the Egg and Temperature and the Growth of the Frog, SERGIUS MORGULIS, 57
Chapman, F. M., Life History of the Booby, WILLIAM E. RITTER, 700
Chondriosomes as Bearers of the Hereditary Qualities, F. PAYNE, 190
Chromosomes, The Permanence of,

in Plant Cells, BRADLEY M. DAVIS, 571
Chub and the Texas Horn Fly, ROY L. MOODIE, 186
CLARK, AUSTIN HOBART, Chadwick on Red Sea Crinoids, 253; Non-muscular Articulations of, 577; Affinities of the Echinoidea, 682
Clark, H. L., The Apodous Holothurians, W. K. FISHER, 111
CLEMENTS, FREDERIC E., Darwin's Influence on Plant Geography and Ecology, 143
Climatic Factors and Vegetation, EDGAR TRANSEAU, 487
COCKERELL, T. D. A., Tutt on Blue Butterflies of the Genus Celastrina, 114
COKER, W. C., Vitality of Pine Seeds, 677
Collinge, Walter E., Experiments in Breeding Slugs, T. D. A. COCKERELL, 510
Color Sense in the Honey Bee, JOHN H. LOVELL, 338
Conklin, E. G., Linerges mercurius, WILLIAM E. RITTER, 699
Constants, Biometric, Degree of Accuracy of, RAYMOND PEARL, 238
COOK, HAROLD JAMES, Camel from the Lower Miocene of Nebraska, 188
COOK, O. F., Pure Strains as Artifacts of Breeding, 241
Copulation among Crawfishes, with Special Reference to Sex Recognition, A. S. PEARSE, 746
Correlation, Organic, A Mechanism for, G. H. PARKER, 212
Correns on Variegation, W. J. SPILLMAN, 442
COULTER, JOHN M., Vascular Anatomy and the Reproductive Structures, 219
COWLES, HENRY C., Ecological Philosophy, 356
COWLES, R. P., The Sand-Crab, 699
COX, CHARLES F., Charles Darwin and the Mutation Theory, 65
Crawfishes, Copulation among, with Special Reference to Sex Recognition, A. S. PEARSE, 746
Cray Fish, Male with some Female Organs, E. A. ANDREWS, 461
Crinoids, Non-muscular Articulations of, AUSTIN HOBART CLARK, 577
Cross Pollination in Plants, Darwin's Work on, WILLIAM TRELEASE, 131
Cuénot, L., Drone Eggs of the Honey Bee, T. H. MORGAN, 316; Inheritance of Color in Mice, T. H. MORGAN, 494
Cunningham on "Hormones," FRANK E. LUTZ, 249
Cuticula and Sub-Cuticula of Trematodes and Cestodes, HENRY S. PRATT, 705

DALL, WILLIAM HEALEY, The Molluscan Fauna of the Peruvian Zoological Province, 532
Darwin, Charles, and the Mutation Theory, CHARLES F. COX, 65; as a Naturalist; Darwin's Work on Cross Pollination in Plants, WILLIAM TRELEASE, 131; Influence on Plant Geography and Ecology, FREDERIC E. CLEMENTS, 143; Work on Movement in Plants, HERBERT MAULE RICHARDS, 152; The Origin of Species in the Light of Recent Observation and Experiment, EDWIN LINTON, 163
DAVENPORT, CHARLES B. and GERTRUDE C., Heredity of Hair Color in Man, 193
DAVENPORT, C. B., Degeneration accompanying Inbreeding, 764
DAVIS, BRADLEY M., Schenck on the Origin of the Archegoniates, 107; The Permanence of Chromosomes in Plant Cells, 571
Dawson, E. Rumley, on the Causation of Sex, H. E. JORDAN, 756
DEDERER, PAULINE H., Cænolestes, Polyprodonta and Diprodonta, 614
Degeneration accompanying Inbreeding, C. B. DAVENPORT, 764
Development and Heredity in Inbreeding, EDWARD M. EAST, 173
DeVries's Species and Varieties, GEORGE H. SHULL, 383
Dinichthyd Armor Plates, BURNETT SMITH, 588
Distribution, Local, on Arid Regions, VOLNEY M. SPALDING, 472
Domestic Fowl, Notes on the Behavior of, PHILIP B. HADLEY, 669
Durham, F. M., Coat Colors in Mice, T. H. MORGAN, 494

EAST, EDWARD M., The Distinction between Development and Heredity in Inbreeding, 173
East, E. M., Inheritance in Sweet Corn, W. J. SPILLMAN, 448
Echinodermata, 253
Echinoidea, Affinities of, AUSTIN HOBART CLARK, 682
Ecological Philosophy, HENRY C. COWLES, 356

Ecology, and Plant Geography, Darwin's Work on, WILLIAM TRELEASE, 143; Entomology of the Indian Corn Plant, S. A. FORBES, 286; Physiological Plant, BURTON LIVINGSTON, 369; Plant, Present Problems in, CHARLES H. SHAW, 420
Entomological Ecology of the Indian Corn Plant, S. A. FORBES, 286
Environment, the Effect of, on Animals, FRANK E. LUTZ, 248
Errera, Leo, In Memoriam, CHARLES E. BESSEY, 640
Evolution, Notes on, VERNON L. KELLOGG, 379; Poulton and Plate on, V. L. KELLOGG, 317
Experimental, Evolution, 55; Zoology, 57, 251, 316, 494, 702

Federly on the Scales of Lepidoptera, FRANK E. LUTZ, 55
FISHER, W. K., H. L. Clark's The Apodous Holothurians, 111
Flora of Krakatau, DOUGLAS HOUGHTON CAMPBELL, 449
FORBES, S. A., Entomological Ecology of the Indian Corn Plant, 286
Fowl, Domestic, The Behavior of, PHILIP B. HADLEY, 669
Frog's Egg, the Totipotence of the First Two Blastomeres of, J. F. MCCLENDON, 384
Fuhrmann on the Cestodes of Birds, HENRY B. WARD, 62

GRIGGS, ROBERT F., Juvenile Kelps and the Recapituiation Theory, 5, 92
Growth, Recent Studies on, RAYMOND PEARL, 302

HADLEY, PHILIP B., The Behavior of the Domestic Fowl, 669
Haeckel and the Phyletic Museum at Jena, VERNON L. KELLOGG, 379
Hagedoorn, A. L., Inheritance of Yellow Color in Rodents, T. H. MORGAN, 505
Hair Color in Man, Heredity of, GERTRUDE C. DAVENPORT and CHARLES B. DAVENPORT, 193
Harben Lectures, HENRY B. WARD, 63
HARRIS, J. ARTHUR, Variation in the Number of Seeds per Pod in the Broom, 350; Selective Elimination of Ovaries in the Fruiting of the Leguminosæ, 556; Note of the Prairie-dog Owl, which resembles the Rattlesnake's Rattle, 764
Heckel on Cultural Bed Mutations in the Potato, 192
Heredity, 190, 243, 437; and Development in Inbreeding, EDWARD M. EAST, 173; of Hair Color in Man, GERTRUDE C. DAVENPORT and CHARLES B. DAVENPORT, 193; and Variation in the Simplest Organisms, H. S. JENNINGS, 321; Non-Mendelian, a Case of, W. J. SPILLMAN, 437
HILTON, WILLIAM A., Batrachoceps attenuatus and Autodax lugubris in Southern California, 53
HOLMES, S. J., Categories of Variation, 257
Holothurians, 111
Hornaday's Camp-fires on Desert and Lava, ROY L. MOODIE, 127
Horse Sires, Age of Trotting, F. R. MARSHALL, 50
HORTON, B. B., Inheritance of Color in Pigeons, 702
Huene, F. Von, Callibrachion, ROY L. MOODIE, 123
Hybridology and Gynandromorphism, T. H. MORGAN, 251

Ichthyology, Notes on, DAVID STARR JORDAN, 560
Inbreeding, Development and Heredity in, EDWARD M. EAST, 173; Degeneration accompanying, C. B. DAVENPORT, 764
Inheritance, of Coat Colors in Mice, T. H. MORGAN, 494; of Color in Pigeons, B. B. HORTON, 702

Janet, Pierre, Les Nevroses, VERNON L. KELLOGG, 381
JEFFREY, EDWARD C., The Progress of Plant Anatomy during the Last Decade, 230.
JENNINGS, H. S., Heredity and Variation in the Simplest Organisms, 321; Bohn's the Birth of Intelligence, 619
Jennings, H. S., Acquired Characters in Protozoa, FRANK E. LUTZ, 251; VERNON L. KELLOGG, 382
JOCHELSON, WALDEMAR, Traditions in Northeastern Siberia about the Mammoth, 48
JORDAN, DAVID STARR, Notes on Ichthyology, 560
JORDAN, H. E., E. Rumley Dawson on the Causation of Sex, 756
Jordan, H. E., Germinal Spot in Echinoderm Eggs, WM. E. RITTER, 694

KELLICOTT, W. E., Growth of Brain and Viscera in the Dogfish, RAYMOND PEARL, 306
KELLOGG, V. L., Poulton and Plate on Evolution, 317
Kellogg, V. L., Inheritance in Silkworms, W. J. SPILLMAN, 445
Kelps, Juvenile, and the Recapitulation Theory, ROBERT F. GRIGGS, 5, 92
Kleine on Nagana, H. B. WARD, 568
Krakatau, The New Flora of, DOUGLAS HOUGHTON CAMPBELL, 449

Larva and Spat of the Canadian Oyster, J. STAFFORD, 31
Land Connection, An Early Tertiary, between North and South America, R. F. SCHARFF, 513
Leguminosæ, Selective Elimination of Ovaries in the Fruiting of the, J. R. HARRIS, 556
Lepidoptera, 114
LINTON, EDWIN, Darwin's Origin of Species in the Light of Recent Observation and Experiment, 163
Linton, Edwin, Parasitic Worms, WILLIAM E. RITTER, 698
LIVINGSTON, BURTON, Physiological Plant Ecology, 369
LOVELL, JOHN H., The Color Sense in the Honey Bee, 338
Lundegardh, H., Origin of the Bivalent Chromosomes, BRADLEY M. DAVIS, 573
LUTZ, FRANK E., The Effect of the Environment upon Animals, 55, 248

MCCLENDON, J. F., Frog's Egg, the Totipotence of the First Two, 384
McClung, C. E., Bison occidentalis, ROY L. MOODIE, 123
Mammalogy, 633
Mammoth, Traditions about, in Northeastern Siberia, WALDEMAR JOCHELSON, 48
Marchal on Environmental Effect, FRANK E. LUTZ 56
Marine Biology, 694
MARSHALL, F. R., Age of Trotting Horse Sires, 50
Mayer, A. G., Tortugas Laboratory of the Carnegie Institution, WILLIAM E. RITTER, 693; Cassiopea, 699
Merriam, J. C., Nectosaurus, ROY L. MOODIE, 123
Meves on Chondriosomes as Bearers of the Hereditary Qualities, F. PAYNE, 190
Mice, The Inheritance of Coat Colors in, T. H. MORGAN, 494
MILLER, NEWTON, The American Toad, 641, 730
Molluscan Fauna of the Peruvian Zoological Province, WILLIAM HEALEY DALL, 532
MOODIE, ROY L., The Lysorophidæ, 116; Hugo Schwarz on Stegocephala, 119; Williston and Broili on the Cotylosauria, 121; The Oldest Known Reptile, 122; Broili on the Age of the Gaskohle, 122; McClung on Bison occidentalis, 123; J. C. Merriam on Nectosaurus, 123; F. von Huene on Callibrachion, 124; Hornaday's Camp-fires on Desert and Lava, 127; The Chub and the Texas Horn Fly, 186
MORGAN, T. H., Breeding Experiments with Rats, 182; Hybridology and Gynandromorphism, 251; Cuénot on the Drone Eggs of the Honey Bee, 316; Inheritance of Coat Colors in Mice, 494
MORGULIS, SERGIUS, Robert Chambers on the Size of the Egg and Temperature and Growth of the Frog, 57
Movement in Plants, Darwin's Work on, HERBERT MAULE RICHARDS, 152
Mutation Theory and Charles Darwin, CHARLES F. COX, 65

Note of the Prairie-dog Owl, which resembles the Rattlesnake's Rattle, J. ARTHUR HARRIS, 764
Notes and Literature, 55, 107, 190, 256, 301, 379, 437, 494, 619, 694

Organic Correlation, A Mechanism for, G. H. PARKER, 212
Orthogenesis, The Theory of, ALEXANDER G. RUTHVEN, 401
Osgood's Revision of the Genus Peromyscus, J. A. ALLEN, 633
Ovaries, Selective Elimination of, in the Fruiting of the Leguminosæ, J. Arthur HARRIS, 556
OVERTON, J. B., Permanence of Chromosomes, BRADLEY M. DAVIS, 572
Owl, Prairie-dog, Note which resembles the Rattlesnake's Rattle, J. ARTHUR HARRIS, 764
Oyster, Canadian, Larva and Spat of, J. SAFFORD, 31

Parasitology, 62, 567
PARKER, G. H., A Mechanism for Organic Correlation, 212
Patton on Herpetomonas, H. B. WARD, 570

PAYNE, F., The Chondriosomes as Bearers of the Hereditary Qualities, 190
PEARL, RAYMOND, Accuracy of the Biometric Constants, 238; Donaldson's Studies on Growth, 302; and FRANK M. SURFACE, Selection Index Numbers and their Use in Breeding, 385
PEARSE, A. S., Copulation among Crawfishes, with Special Reference to Sex Recognition, 746
Perkins, H. F., Medusæ, WILLIAM E. RITTER, 697
Peruvian Zoological Province, Molluscan Fauna of, WILLIAM HEALEY DALL, 532
Pigeons, Inheritance of Color in, B. B. HORTON, 702
Pine Seeds, Vitality of, W. C. COKER, 677
Plant, Phylogeny, 107; Cytology, 571; Anatomy, Progress during the Last Decade, EDWARD C. JEFFREY, 230
Pleistocene Swamp Deposits in Virginia, EDWARD W. BERRY, 432
Pollination, Cross, in Plants, Darwin's Work on, WILLIAM TRELEASE, 131
Potato, Heckel on Cultural Bed Mutations in, 192
Poulton and Plate on Evolution, V. L. KELLOGG, 317
POWERS, J. H., Are Species Realities or Concepts only? 593
Powers on the Variation in Amblystoma tigrinum, 56
PRATT, HENRY S., The Cuticula and Sub-Cuticula of Trematodes and Cestodes, 705
Presence and Absence Hypothesis, GEORGE HARRISON SHULL, 410
Psychology, Comparative, 619

Raepke, W., on Hybridology and Gynandromorphism, T. H. MORGAN, 251
Rats, Breeding Experiments with, T. H. MORGAN, 182
Recapitulation Theory and Juvenile Kelps, ROBERT F. GRIGGS, 5, 92
Reighard, Jacob, Warning Coloration, WILLIAM E. RITTER, 701
Reproductive Structures and Vascular Anatomy, JOHN M. COULTER, 219
RICHARDS, HERBERT MAULE, Darwin's Work on Movement in Plants, 152
Riddle, O., Melanin Color Formation, T. H. MORGAN, 509
RITTER, WILLIAM E., Tortugas Laboratory of the Carnegie Institution, 693
Robertson, T. B., The Normal Rate of Growth, RAYMOND PEARL, 309
Rosenberg, O., Permanence of Chromosomes, BRADLEY M. DAVIS, 573
RUTHVEN, ALEXANDER G., The Theory of Orthogenesis, 401

SCHARFF, R. F., An Early Tertiary Land Connection, between North and South America, 513
Schenck, H., The Origin of the Archegoniates, BRADLEY M. DAVIS, 107
Schwarz, Hugo, on Stegocephala, ROY L. MOODIE, 119
Seeds, Number per Pod in the Broom, J. ARTHUR HARRIS, 350
Sex, Recognition, Copulation among Crawfishes, with special reference to, A. S. PEARSE, 746; the Causation of, E. Rumley Dawson on, H. E. JORDAN, 756
SHAW, CHARLES H., Present Problems in Plant Ecology, 420
Shorter Articles and Correspondence, 48, 186, 238, 432, 611
SHULL, GEORGE H., DeVries's Species and Varieties, 383; "Presence and Absence" Hypothesis, 410
Sleeping Sickness Bureau, HENRY B. WARD, 124
Slugs, Experiments in Breeding, T. D. A. COCKERELL, 510
SMITH, BURNETT, Dinichthyd Armor Plates, 588
SPALDING, VOLNEY M., Local Distribution on Arid Regions, 472
Species, Are they Realities or Concepts only? J. H. POWERS, 593
SPILLMAN, W. J., The Nature of Unit Characters, 243, Heredity, 437
STAFFORD, J., Larva and Spat of the Canadian Oyster, 31
Starfishes on the Northwest American Coast, A. E. VERRILL, 542
STOCKARD, CHAS. R., Regeneration, 696; Aplopus mayeri, 699
SURFACE, FRANK M., and RAYMOND PEARL, Selection Index Numbers and their Use in Breeding, 385
Swamp Deposits, Pleistocene, in Virginia, EDWARD W. BERRY, 432

Tertiary Land Connection between North and South America, R. F. SCHARFF, 513
Toad, The American, NEWTON MILLER, 641, 730

Tortugas Laboratory of the Carnegie Institution, WILLIAM E. RITTER, 693
Traditions in Northeastern Siberia about the Mammoth, WALDEMAR JOCHELSON, 48
TRANSEAU, EDGAR, Climatic Factors and Vegetation, 487
TRELEASE, WILLIAM, Darwin as a Naturalist; Darwin's Work on Cross Pollination in Plants, 131
Trematodes and Cestodes, The Cuticula and Sub-Cuticula of, HENRY S. PRATT, 705
Trotting Horse Sires, Age of, F. R. MARSHALL, 50
Tutt, J. W., Blue Butterflies of the Genus Celastrina, T. D. A. COCKERELL, 114

Variation, Categories of, S. J. HOLMES, 257; and Heredity in the Simplest Organisms, H. S. JENNINGS, 321; in the Number of Seeds per Pod in the Broom, J. ARTHUR HARRIS, 350
Vascular Anatomy and the Reproductive Structures, JOHN M. COULTER, 219
Vegetation and Climatic Factors, EDGAR TRANSEAU, 487
VERRILL, A. E., Development of Starfishes on the Northwest American Coast, 542
Vertebrate Paleontology, 116
Vitality of Pine Seeds, W. C. COKER, 677

WARD, HENRY B., The Cestodes of Birds, 63; The Sleeping Sickness Bureau, 124; Parasitology, 567
WATSON, J. B., Behavior of Noddy and Sooty Terns, 700
Whitney, D. D., Development and Sex, W. J. SPILLMAN, 444
Williston on the Lysorophidæ, 116; on the Cotylosauria, 121; on the Oldest Known Reptile, ROY L. MOODIE, 122
Wilson, E. B., on Chromosomes and Hereditary Characters, W. J. SPILLMAN, 240
WRIGHT, ALBERT H., and ARTHUR ALLEN, Breeding Habits of Amblystoma punctatum, 687

The American Naturalist

A Monthly Journal, established in 1867, Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Organic Evolution and Heredity

CONTENTS OF THE JUNE NUMBER

Heredity and Variation in the Simplest Organisms. Professor H. S. JENNINGS.

The Color Sense of the Honey Bee — Is Conspicuousness an Advantage to Flowers? JOHN H. LOVELL.

Variation in the Number of Seeds per Pod in the Broom, Cytisus scoparius. Doctor J. ARTHUR HARRIS.

resent Problems in Plant Ecology:

The Trend of Ecological Philosophy. Professor HENRY C. COWLES.

The Present Problems of Physiological Plant Ecology. DR. BURTON LIVINGSTON.

Notes and Literature: Notes on Evolution, V. L. K. DeVries's Species and Varieties, DR. GEORGE H. SHULL. *Embryology* — On the Totipotence of the First Two Blastomeres of the Frog's Egg. DR. J. F. McCLENDON.

CONTENTS OF THE JULY NUMBER

Selection Index Numbers and their Use in Breeding. Dr. RAYMOND PEARL and FRANK M. SURFACE.

A Contribution to the Theory of Orthogenesis. Dr. ALEXANDER G. RUTHVEN.

The "Presence and Absence" Hypothesis. Dr. GEORGE HARRISON SHULL.

Present Problems in Plant Ecology: Vegetation and Altitude. Professor CHARLES H. SHAW.

Shorter Articles and Correspondence: Pleistocene Swamp Deposits in Virginia. Dr. EDWARD W. BERRY.

Notes and Literature: *Heredity*—A Case of Non-Mendelian Heredity. Dr. W. J. SPILLMAN.

CONTENTS OF THE AUGUST NUMBER

The New Flora of Krakatau. Professor DOUGLAS HOUGHTON CAMPBELL.

A Male Crayfish with Some Female Organs. Professor E. A. ANDREWS.

Present Problems in Plant Ecology:

Problems of Local Distribution on Arid Regions. Professor VOLNEY M. SPAULDING.

The Relation of the Climatic Factors to Vegetation. Professor EDGAR N. TRANSEAU.

Notes and Literature: Recent Experiments on the Inheritance of Coat Colors in Mice, Professor T. H. MORGAN. Some Experiments in Breeding Slugs. Professor T. D. A. COCKERELL.

CONTENTS OF SEPTEMBER NUMBER

On an Early Tertiary Land-connection between North and South America. Dr. R. F. SCHARF.

Notes on the Relations of the Molluscan Fauna of the Peruvian Zoological Province. Dr. WILLIAM HEALEY DALL.

Remarkable Development of Starfishes on the Northwest American Coast; Hybridism; Multiplicity of Rays; Teratology; Problems in Evolution; Geographical Distribution: Professor A. E. VERRILL.

Shorter Articles and Correspondence: Is there a Selective Elimination of Ovaries in the Fruiting of the Leguminosæ: Dr. R. HARRIS.

Notes and Literature: *Ichthyology*—Ichthyological Notes, President DAVID STARR JORDAN. *Parasitology* — Professor H. B. WARD. *Plant Cytology*—The Permanence of Chromosomes in Plant Cells, Dr. BRADLEY M. DAVIS.

CONTENTS OF THE OCTOBER NUMBER

The Non-muscular Articulations of Crinoids. AUSTIN HOBART CLARK.

On Some Dinichthyid Armor Plates from the Marcellus Shale. BURNETT SMITH.

Are Species Realities or Concepts only. Professor J. H. POWERS.

Shorter Articles and Discussion: A Light Weight, Portable Outfit for the Study and Transportation of Ants. EDITH N. BUCKINGHAM. Comparison of Cænolestes with Polyprotodonta and Diprotodonta. PAULINE H. DEDERER.

Notes and Literature: *Comparative Psycholoy* — Bohn's "The Birth of Intelligence": Professor H. S. JENNINGS. *Mammalogy*—Osgood's Revision of the Mice of the Genus Peromyscus, Dr. J. A. ALLEN, LEO ERRARA, Professor CHARLES E. BESSEY.

CONTENTS OF THE NOVEMBER NUMBER

The American Toad (Bufo lentiginosus americanus LeConte). NEWTON MILLER.

Notes on the Behavior of the Domestic Fowl. PHILIP B. HADLEY.

Vitality of Pine Seeds and the Delayed Opening of Cones. Professor W. C. COKER.

The Affinities of the Echinoidea. AUSTIN HOBART CLARK.

The Early Breeding Habits of Amblystoma punctatum.

Notes and Literature: *Marine Biology*—Papers from the Tortugas Laboratory, Professor WILLIAM E. RITTER. *Experimental Evolution* — Inheritance of Color in Pigeons, B. B. HORTON.

Single Number 35 Cents **Yearly Subscription, $4.00**

The NATURALIST will be sent to new subscribers for four months for One Dollar

THE SCIENCE PRESS

Garrison, N. Y. **Sub-Station 84: NEW YORK** **Lancaster, Pa.**

Neurological Technique

By IRVING HARDESTY

196 pages, 8vo, cloth ; net $1.75, postpaid $1.87

INTENDED to serve as an introduction and laboratory guide to the study of the architecture of the nervous system, containing a succinct account of methods which have stood the test of practical application.

"The instructions are thoroughly practical."—*British Medical Journal.*

"We know of no similar book which will be as valuable to the student of neurological technique."—*American Journal of Insanity.*

"The descriptions are clear." — *Philadelphia Medical Journal.*

"The book bears the indorsement of Henry Donaldson, which is sufficient guarantee for its widespread acceptance."—*Northwestern Lancet.*

Laboratory Outlines for the Study of the Embryology of the Chick and the Pig

By FRANK R. LILLIE

60 pages, 12mo, paper ; net 25 cents, postpaid 27 cents

WILL be found a valuable contribution toward the establishment of a standard of embryological work for students generally, and for others desiring a convenient guide to the order of study of this subject.

Quantitative Classification of Igneous Rocks

Based on Chemical and Mineral Characters, with a Systematic Nomenclature

By WHITMAN CROSS, JOSEPH P. IDDINGS, LOUIS V. PIRSSON and HENRY S. WASHINGTON

286 pages, 8vo, cloth ; net $1.75, postpaid $1.91

AN entirely new system for the classification and nomenclature of igneous rocks according to chemico-mineralogical principles, accompanied by a complete original nomenclature adapted to the system. Of value to all geologists and petrologists.

The Rôle of Diffusion and Osmotic Pressure in Plants

By BURTON EDWARD LIVINGSTON

160 pages, 8vo, cloth ; net $1.50, postpaid $1.62

THE important part played by the phenomena connected with diffusion and osmotic pressure in the life-process has here for the first time found full and adequate treatment.

Address Dept. 62

THE UNIVERSITY OF CHICAGO PRESS

CHICAGO AND NEW YORK